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Title
Qualitative modelling and Bayesian network analysis for risk-based biosecurity decision making in complex systems

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Summary
This project investigates the practical application of Bayesian belief networks and qualitative modelling via two biosecurity case studies. The first uses a Bayesian belief network to identify the factors that determine the success of a Red Import Fire Ant eradication campaign. The second used qualitative modelling to investigate the dynamics of Eucalypt rust infection in subtropical Australian forests. The results of both case studies demonstrate that qualitative modelling and Bayesian belief networks are transparent, repeatable, make predictions that can be experimentally and/or statistically tested, and do not need large amounts of empirical data. Both case studies were based entirely on expert and stakeholder opinion, and provided testable predictions of system behaviour.

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FINAL REPORT

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Disclaimer

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EXECUTIVE SUMMARY

The objectives of this project are to: 1) demonstrate the importance and implications of feedback for risk-based decision making within complex systems; 2) provide a non-technical introduction to the theory and practice of qualitative modelling and Bayesian Belief Networks; 3) demonstrate the utility of these techniques within a biosecurity context; and 4) demonstrate the communication potential of graphical models that are able to incorporate the effects of risk-management decisions.

We investigated the practical application of BBNs and qualitative modelling via two biosecurity case studies. The first used a BBN to identify the factors that determine the success of a Red Import Fire Ant (RIFA) eradication campaign. The second used qualitative modelling to investigate the dynamics of Eucalypt rust infection in subtropical Australian forests.

The RIFA case study successfully developed a conceptual model of the key variables that governed the success of an eradication attempt, and highlighted the importance of correctly predicting the location of RIFA nests particularly in the latter stages of an eradication campaign. It also provided a decision support framework within which the importance of training and commitment among staff could be evaluated, together with the value of information about detection functions and treatment effectiveness

The results of the second case study rust support the concern that Eucalypt rust will have a negative impact on Myrtaceae species in Australian subtropical forests, and this obvious, if not trivial, result was invariant across all fire regimes, and assumptions about susceptibility of different forms of shoot growth. The analysis of qualitative models also supports the hypothesis that natural selection for rust resistance might progress most rapidly in an infrequent-intense fire regime. An important result of this work is that a frequent low-intensity fire regime can potentially mitigate the effects of Eucalypt rust through reduced understorey development and hence humidity.

The results of both case studies demonstrate that qualitative modelling and BBNs are transparent, repeatable, make predictions that can be experimentally and/or statistically tested, and do not need large amounts of empirical data. Both case studies were based entirely on expert and stakeholder opinion, and provided testable predictions of system behaviour. The Eucalypt case study also explicitly explored uncertainty in model structure via a range of competing hypothesis about the dynamics of rust infections in subtropical Australian forests.

The most significant disadvantage of BBNs is the time, expertise and data needed to realistically represent complex spatial and temporal dynamics, including feedback. Realistically complex levels of feedback can be readily analysed using qualitative modelling, but this method cannot identify which of a series of competing models is more likely to be true. Neither of these approaches can replace existing biosecurity risk assessment methods. Both, however, provide a firm scientific foundation for building and analysing conceptual models of complex systems, and as such are an ideal complement to existing approaches, particularly in the early problem formulation stage of an assessment.

• INTRODUCTION

The objective of Australia's biosecurity policy is defined as "the prevention or control of the entry, establishment or spread of pests and diseases that will or could cause significant damage to human beings, animals, plants, other aspects of the environment, or economic activities" (AFFA 2003). The Australian Import Risk Analysis Handbook goes on to define risk assessment as the scientific "evaluation of the likelihood of entry, establishment or spread of a pest or disease within the territory of an importing Member according to the sanitary or phytosanitary measures which might be applied, and of the associated potential biological and economic consequences".

The process of risk evaluation, characterization and management gives an organization a greater degree of control over the potential impacts of, for example, the introduction of non-indigenous species. The classical 'engineering approach' to risk seeks to maximise control through risk management. This approach is characterised by the following assumptions:

- A system exists in a finite set of states that can be controlled;

- Risks can be quantified by multiplying the probability of an event by the consequences; and,

- Uncertainties can be quantified using probabilities.

Ecological risks, however, are often much more ambiguous and difficult to characterize than engineering risks because ecosystems are dynamic, non-linear structures that we do not fully understand. An evaluation of the likelihood of entry, establishment or spread of a pest or disease, for example, involves high degrees of uncertainty and complexity. A different control paradigm, with a revised set of assumptions, may therefore be necessary to assess biosecurity risks. These assumptions might include:

- Ecological systems are complex;

- The effects of ecosystem stressors are determined by *inter alia* the non-linear feedback properties of the ecosystem;

- New methodologies are needed to assess causality and capture structural uncertainties in environmental risk assessment.

This project contributes to the development of tools for improving risk assessment procedures for the Australian Government Department of Agriculture, Fisheries and Forestry (AGDAFF). The objectives of this project are: 1) demonstrate the importance and implications of feedback for risk-based decision making within complex systems; 2) provide a non-technical introduction to the theory and practice of qualitative modelling and Bayesian Belief Networks; 3) demonstrate the utility of these techniques within a biosecurity context; and 4) demonstrate the communication potential of graphical models that are able to incorporate the effects of risk-management decisions.

In this report we introduce Bayesian Belief Networks and qualitative models as tools that can be used to analyse and assess biosecurity risks in complex systems. This report is divided into five sections. The first section (this one) briefly describes the motivation for the project. The second section provides a brief, non-technical introduction to qualitative modelling and Bayesian Belief Networks as ways to develop and analyse conceptual models of complex ecological systems. This section highlights examples where these techniques have been used in biosecurity and natural resource management contexts. The third and fourth section report on two biosecurity case studies that demonstrate how qualitative models and Bayesian Belief Networks can assist management authorities to assess and manage the risks associated with diseases and introduced species. The fifth, final, section summarises the results of the cases studies and makes a number of concluding remarks.

- # CONCEPTUAL MODELS IN RISK ASSESSMENT

- ## Conceptual models of complex systems

Biosecurity risks assessment entails complex models of the various cultural, ecological and socio-economic factors that influence the introduction, establishment and spread of diseases and invasive species. These models are complex because of the multiple direct and indirect connections between the cultural, ecological and socio-economic factors that determine the course of biological invasions.

All models are abstractions of reality based on the model builder's conceptions. The utility of a model is partially dependant on the accuracy of this conception (the conceptual model). All risk assessments are structured (implicitly or explicitly) around a conceptual model of the system in question. In risk assessment, conceptual models are representations of the hypothesized mechanisms by which an activity or set of activities induce effects on the risk assessment endpoints. They often summarize the results of the problem formulation phase of a risk assessment in terms of the cause and effect relationships that link stressors to the assessment endpoints (Suter 1999). Risk assessments can be incomplete, vague and ambiguous if the process of building and analysing conceptual models is not carefully completed.

Creating accurate conceptual models for biosecurity risk assessment can be arduous task due to the innate complexity of the systems involved and our limited understanding of these systems. A strategy is therefore needed for conceptual model building that can handle the complexity of ecosystems and potentially address our knowledge uncertainty about the structure of these systems. Moreover this strategy and methodology should be able to represent the complexities of the system whilst remaining clear, comprehensible and integrated with more quantitative approaches to risk assessment.

Quantitative approaches to risk assessment are often associated with good scientific understanding and numerical information, while qualitative approaches are usually associated with incomplete understanding, a lack of numerical data and verbal representations of information. Qualitative information is often perceived as the vague, messy and the highly uncertain underdog to quantitative data. In the absence of data or in the face of incomplete, vague or ambiguous knowledge, however, the quest for precision can actually be counter productive and produce meaningless risk metrics.

Puccia and Levins (1985) state that the primary goal of qualitative modelling is understanding rather than numerical prediction. Qualitative modelling sacrifices precision for realism and generality and focuses on the relationships between model variables. Our current understanding of complex systems often precludes confident numerical prediction. Developing a better understanding of these systems, through qualitative modelling, may therefore provide a useful complement to the more usual numerical approaches when evaluating biosecurity risks in ecological systems. In the following sections we describe two methods that can be used to develop analyse conceptual models of complex systems: qualitative modelling and Bayesian Belief Networks.

- ## Qualitative Modelling

- ## Background

Qualitative modelling is a method developed by Richard Levins (1974, 1975). It proceeds by first determining system structure, which is defined by the variables of the system and the relationships by which they are linked. In biological systems, variables are typically interacting populations of different species, and their dynamics can be accounted for by generalized Lotka–Volterra equations, wherein each contributes towards the birth or death of another. Similarly, the dynamics of social and economic systems can be described by the interactions of different sectors and entities of society (such as governing bodies, social customs, and markets) that control flows of resources, goods, and services that are either measurable, such as money, or immeasurable, such as status and world view.

- ## Constructing a qualitative model

The variables and relationships in a qualitative model are portrayed by sign-directed graphs, or signed digraphs (SDGs), where a link from one variable to another ending in an arrow ($\rightarrow$) represents a positive direct effect, such as births produced by consumption of prey, and a link ending in a filled circle ($\rightarrow\bullet$) represents a negative direct effect, such as death from predation. All possible relationships can be described in this manner. Ecological relationships, for example, are portrayed in the following manner: predator–prey or parasitism ($\bullet\rightarrow$), mutualism ($\leftrightarrow$), commensalism ($\rightarrow$), interference competition ($\bullet\!-\!\bullet$), and amensalism ($-\!\bullet$). Self-effects are shown by links originating and ending in the same variable, and are typically negative ($\circlearrowleft$), as in self-regulated variables, but can also be positive ($\circlearrowright$) where variables are self-enhancing.

Figure 1 shows a SDG of a real host-parisitoid community studied by Borer et al. (2003). Red scale *Aonidiella aurantii* is a common non-native insect pest of orange, grapefruit, and lemon crops in California that is parasitized by two non-native wasps - *Encarsia perniciosi* and *Aphytis melinus*. Unparasitized red scale hosts (N_1) are transferred into a parasitized state following an attack by either *E. perniciosi* (N_2) or *A. melinus* (N_3). These parasitoids are assumed to attack scale hosts at a rate proportional to the number of scale hosts already parasitized; this produces a predator-prey type relationship of parasitized hosts on their "prey", the unparasitized hosts. In another predator-prey type relationship, attacks by *A. melinus* on scale hosts already parasitized by *E. perniciosi* are assumed to transfer these hosts into a state of parasitization by *A. melinus*. All three variables exhibit intraspecific density-dependent growth; for unparasitized hosts it is via intra-specific competition for the basal citrus resource (Borer et al. 2003, 2004; Murdoch et al. 2005).

Having constructed one or more SDGs, qualitative modelling allows the analyst to determine whether or not the system is likely to be stable, and therefore theoretically capable of persisting in the state described by the SDG, and also to predict the effects of a sustained disturbance to the system (otherwise known as a press perturbation). The predictions are summarised within the adjoint or "prediction" matrix that indicates the direction of change (increase, decrease or no change) for each variable in the SDG, based on the direct and indirect interactions within the system. Indirect interactions are very important in this context because they capture the (often counterintuitive) effects caused by feedback in the SDG. Appendix A discusses in more detail the methods for determining qualitative stability and the effects of a press perturbation.

Dambacher et al. (2002, 2003a, 2003b) and Hosack et al. (in prep) provide a detailed treatment of the matrix algebra methods that underlie qualitative modelling methods.

Figure 1   A simple signed digraph of a host-parasitoid community in Californian citrus crops (from Borer et al. 2003)
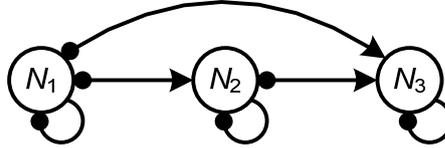
Two of the most important advantages of qualitative modelling is that SDGs can be generated (and analysed) much more quickly than an equivalent size numerical model, and the modelling is much more amenable to stakeholder input because it is (at least in the first instance) entirely graphical and does not require sophisticated mathematical skills. Furthermore, by focussing on the qualitative, as opposed to the quantitative, relationship between variables, qualitative modelling foregoes the pre-occupation with parametric uncertain and encourages the analyst to identify and incorporate structural (model) uncertainty into the early stages of a risk assessment. An analyst can easily identify multiple SDGs to represent different plausible model structures and/or different stressors and management regimes (see section   ).

- **Applications**

Qualitative modelling has been applied to a diverse number of fields including: planktonic, intertidal and subtidal marine communities (Ascioti and Puccia 1988, Lane 1998, Ortiz 2002), introduced species in aquatic systems (Li and Moyle 1981, Li et al. 1999), tropical forest communities (Giavelli and Bodini 1990) and management of shellfish populations (Whitlatch and Osman 1994).

Loiselle et al. (2000) use qualitative modelling to help design environmental management and monitoring programmes for large complex natural reserves, where little or no quantitative data are available. The authors highlight a number of advantages of this approach especially as a method to highlight potential feedback mechanisms and secondary effects of management actions on a number of key species in a large wetland.

- ## **Bayesian Belief Networks**

- ## **Background**

Bayesian Belief Networks (BBNs) are similar to the qualitative models discussed in Section 2.2, in that both approaches begin with a graphical depiction of the cause-effect relationships among the most important variables in the system of interest. Hence both approaches can be used to provide a graphical representation of the conceptual model that captures the analyst(s) beliefs in the cause and effect pathways that link stressors to assessment endpoints (Figure 2).

Figure 2   Graphical representation of a hazard assessment showing the potential effects of land use management, climate change and marine farming (stressors) on the shore carrying capacity (assessment endpoint) of the Firth of Thames, New Zealand. Dashed lines represent the effects of marine farming which were subsequent used to develop a BBN (from Gibbs 2007)
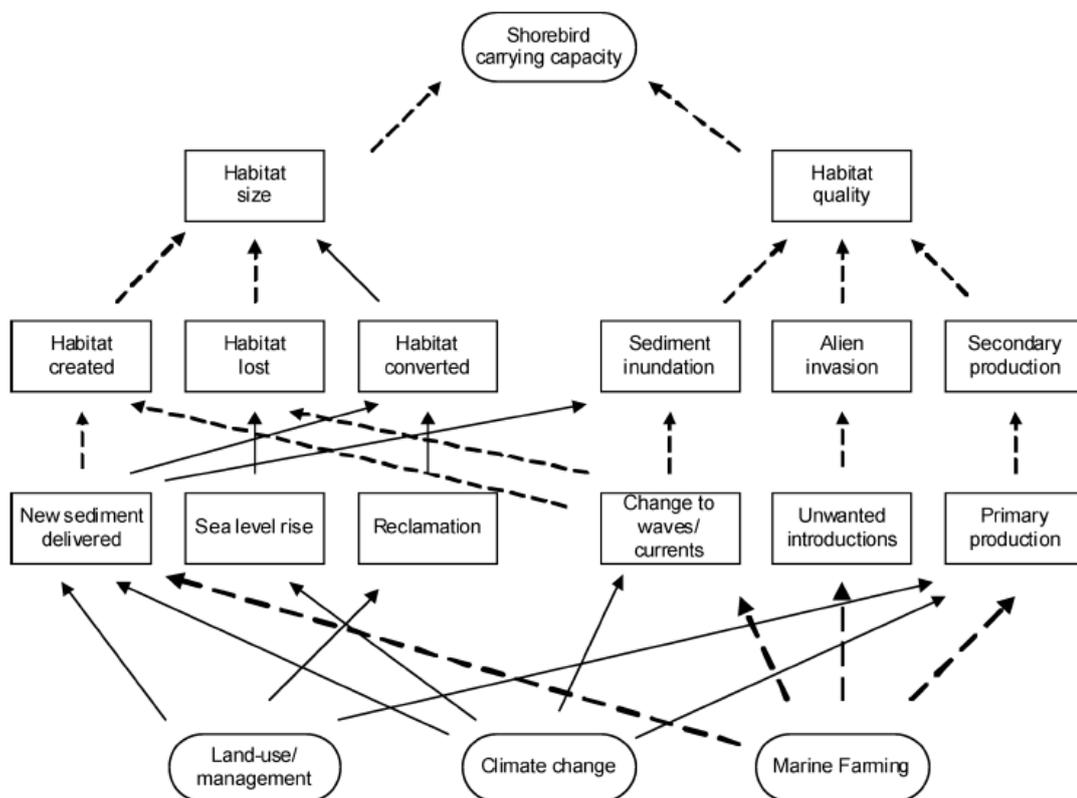
In a BBN the system variables are called "nodes", and the dependences between variables are represented by arrows. Unlike qualitative modelling, the relationships between variables in a BBN are strictly one-way because they represent a conditional probability distribution that describes the relative likelihood of each value of the "child" node (end of the arrow) conditional on every possible combination of values of the "parent" nodes (start of each arrow). Furthermore the co1nditional relationships in a BBN are acyclic – i.e., a path traced along its links cannot pass through a variable more than once. Hence graphical depictions of BBNs are often described as Directed Acyclic Graphs (DAGs) (Pearl 2000) and cannot represent feedback in the system in question without explicitly constructing separate DAGs to represent different time steps in a continuous process (see for example Cain 2001).

- ### **Constructing a Bayesian Belief Network**

Belief networks are comprised of three elements: a set of nodes representing the key variables; a set of links that represent the cause-effect relationship ('conditional dependence') between these nodes; and a set of probabilities representing the belief a node will be in a given state given the states of the connecting nodes (Figure 3). As noted above the first two elements provide a graphical conceptual model of the system in question. One of the important advantages of BBNs is that the last element, the conditional probability relationships, may be based on any available information, including experimental or field results, process-based models, or the (ideally) carefully elicited judgment (beliefs) of scientists and other relevant stakeholders (Borsuk et al. 2006).

Figure 3   A simple Bayesian Belief Network showing the variables, and the relationships between them, that are thought to govern crop yields (from Cain 2001)
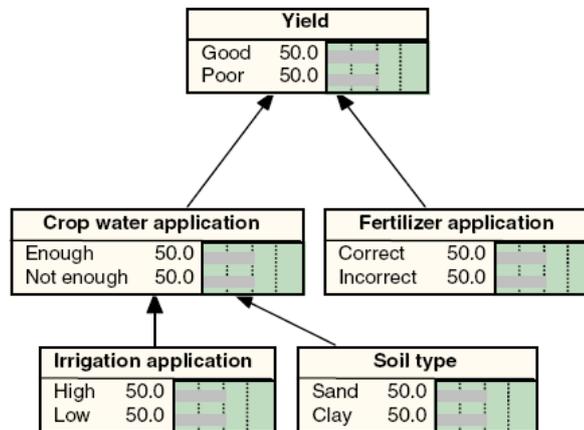
BBNs are usually constructed in an iterative multi-stage process. In the first stage, the analyst constructs the DAG by identifying the important nodes (physical, biological, social, economic or institutional variables), the states of each node and relationships between them. This stage is usually based on existing literature, stakeholder consultation and/or the analyst's experience and knowledge of the system in question. The analyst must then complete the Conditional Probability Tables (CPTs) for the DAG – i.e., the relative likelihood of each value of the "child" node conditional on every possible combination of values of the "parent" nodes. It is important to note that for large BBNs these tables may require many conditional probability assignations, and can therefore be difficult and cumbersome to complete. The CPTs can be completed using empirical observations, model output or the beliefs of the analyst and/or stakeholders.

Various iterations of this process may occur in order to simplify the BBN by, for example, amalgamating nodes, or reducing the number of discrete states within each node, both of which serve to reduce the overall size of the CPTs. These iterations may also include changes to the nodes, their states or indeed the entire DAG to account for discrete time steps in the problem and/or improve the utility of the network. It is important to emphasise that a certain amount of imagination, skill and experience is needed to fully optimise BBNs for management purposes. Cain (2001) provides excellent detailed guidance on the step by step process of constructing and optimising BBNs.

The construction, population and analysis of BBNs is greatly simplified by the availability of commercially available software, such as Netica (http://www.norsys.com/). Netica provides a drag and drop feature that allows an analyst to quickly construct a DAG, and then automatically provides the structure (but not the content!) for the CPT behind each node, once the node states have been manually entered. 1

Netica also includes a sensitivity analysis capability. In general sensitivity analysis determines which inputs (i.e., which variables) most affect the any specified response variable (see for example Marcot 2006). Netica allows the analyst to select a response variable (often called a 'query' node) and produce a report displaying how much the beliefs, mean value, etc. of the query node are influenced by each of the other nodes in the network.

- **Decision networks**

Decisions networks (DNs) are a type of Bayesian network created by adding two special nodes to a BBN. These nodes are:

- Decision Nodes – these represent alternative actions, such as pest control strategies, which are traditionally drawn as rectangular boxes, correspond to variables or events that management agencies can control.

- Utility Nodes – these assign a value to outcomes, for example cost. They can be complex mathematical relationships or simple rankings derived from expert opinion. Utility nodes are drawn with a diamond or flattened hexagon shape, and correspond to quantities that a management agency may wish to maximise or minimise.

A DN represents a decision or planning problem faced by a decision maker. Software packages, such as Netica, can automate the process of find values for the decision nodes that will result in the greatest expected value for the utility node (or sum of them if there is more than one). This is known as "solving" the decision net.

- **Applications**

Bayesian Belief Networks (BBNs) were originally developed in the 1940's and 1950's to allow managers to incorporate the effects of uncertainty in management systems into their decision making process (Henrion et al. 1991). More recently, however, they have been increasingly applied to a variety of natural resource management problems, such as managing water resources (Cain 2001, Pollino et al. 2007), salmon stocks (Varis and Kuika 1997, 1999) and threatened species (Marcot 2006, Marcot et al. 2006).

• BIOSECURITY CASE STUDY I – *SOLENOPSIS INVICTA*

• Background

Red imported fire ants (RIFA), *Solenopsis invicta*, were introduced to the United States from South America around 70 years ago (Vinson 1997) and to Brisbane, Australia in 2001 (Scanlan and Vanderwoude 2006). In the US RIFA are known to cause damage to agricultural crops (Drees et al. 1998), reduce animal production, and damage electrical equipment (Vinson and McKay 1990).

In Australia RIFA stings are recorded as being potentially lethal (Solley et al. 2002) and RIFA colonies are thought to cause significant reductions in native biodiversity. Natrass and Vanderwoude (2001), for example, suggest that RIFA are responsible for significantly reduced ant diversity and the complete absence of scinid lizards in an Australian forest remnant.

In the 'Fire Ant Wars' Buhs (2002) emphasises the unexpected outcomes that occurred when human practices interacted with ant biology, and stresses that analysis that separates human activity from ant biology obscures the critical importance of this interaction in the spread of fire ants in the south of the United States:

"The biology of the ants and human activities interacted in unexpected ways. The ants were not ecological innocents, ready to become well-behaved citizens. They were opportunists, exploiting the disruption brought about by the bulldozer revolution and the constant building in the irrigated West." (Buhs 2002).

• Methods

A number of BBNs were initially constructed for the RIFA case study based on a literature search of the key variables describing RIFA biology and the factors involved in the successful detection and eradication of RIFA nests. These initial hypothetical BBNs were discussed and developed further in a workshop held in Canberra on Thursday, February 22nd, 2007 attended by representatives from several different organisations (Table 1).

The basic objective of the workshop was to identify sound technical information that could form the basis for advice to ministerial council that: a) the Australian RIFA eradication program is on track (or otherwise); and b) the field operations (surveillance and control) best suit the behaviour of the infestation. To explore these issues, the workshop participants were provided with a hypothetical example of a RIFA outbreak in a new location, remote from existing infestations, and asked to develop influence diagrams (conceptual models) that identified the factors that would maximise the chances of successful eradication.

The variables in the influence diagrams develop in the workshop were compared with those identified in the BBNs developed prior to the workshop. A final list of important variables was selected from these two sources and implemented in the RIFA BBN case study. All BBNs were constructed and analysed using the Netica software.

Table 1   Participants at the ACERA sponsored workshop on the use of Bayesian Belief Networks to assist in the management and eradication of Red Imported Fire Ant in Australia

Name	Organisation	Name	Organisation
Mark Burgman	ACERA	Andrew Copp	DEH
Jeffrey Dambacher	CSIRO	Dane Panetta	QDNRM
Keith Hayes	CSIRO	Joe Scanlan	QDNRM
Paul Pheloung	OCPPO	Peter Davis	DAWA
Mike Cole	OCPPO	Fiona Evans	DAWA
Fiona Macbeth	OCPPO	Dennis O'Dowd	Monash University
Stephen Richardson	OCPPO	Will Shenton	Monash University
Elspeth West	OCPPO	Craig Jennings	FICC, QDPIF
Mark Jackson	OCPPO	Darren Kriticos	ENSIS
Stephen Pratt	BRS	Morag Glen	ENSIS
Joe Crombie	BRS		

- ## Results

- ## Hypothetical demonstration

A literature search of the factors that govern successful management and eradication of RIFA nests identified five important variables: the eradication strategy, the time of the year (season), RIFA density and biology, and the complexity of the habitat (see Appendix B). Figure 4 illustrates a simple BBN that uses three of these variables to describe the decision criteria that a management agency might employ when choosing from a range of potential RIFA control options (Appendix C).

Figure 4   A simple Bayesian Belief Network showing the factors that a management agency might believe determine the probability of success of RIFA control options
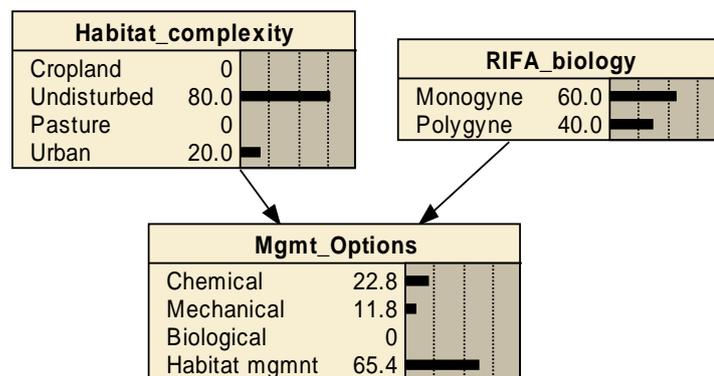
The BBN in Figure 4 encodes the belief that the probability of successfully eradicating a RIFA colony is determined by the biology of the ant colony (monogyne or polygyne), and the type of habitat that the colony occupies (cropland, undisturbed, pasture, urban). The key variables in

this BBN are: a) the type of habitat; b) the ant biology; and, c) the type of control option. The causal links show that the management option is only dependent on the type of habitat the ants are found in and the biology of the ant colony. The conditional relationships between nodes and links is captured in the Conditional Probability Tables (CPTs) that underlie each node. For example, the (hypothetical) conditional probabilities assigned in the 'management options' CPT are shown in Table 2.

Table 2   A CPT showing the (hypothetical) relationships, expressed as conditional probabilities, between the management option nodes and its two parent nodes: habitat type and RIFA biology.

		Management option			
RIFA biology	Habitat type	Chemical	Biological	Mechanical	Habitat mgmnt
Monogyne	Cropland	0.5	0.1	0.15	0.25
Monogyne	Undisturbed	0.1	0.1	0	0.8
Monogyne	Pasture	0.8	0.1	0	0.1
Monogyne	Urban	0.9	0.05	0	0.05
Polygyne	Cropland	0.75	0.1	0.15	0
Polygyne	Undisturbed	0	0.2	0	0.8
Polygyne	Pasture	0.8	0	0.2	0
Polygyne	Urban	0.9	0	0	0.1

The management option CPT expresses the manager's beliefs about the most appropriate management option for all possible combinations of its 'parent nodes'. In this hypothetical example the manager is 90% certain that a chemical management option is most likely to successfully eradicate a monogyne RIFA colony in an urban habitat. The conditional probabilities might also be informed by empirical information on, for example, the frequency of successful management options, under each of the RIFA biology/habitat type combinations.

The CPT of each node of a BBN contains entries, in the form of conditional probabilities, for every possible combination of the states of its parent nodes. Once all these CPTs have been compiled for each node, the network can then be used for analysis. The states of individual nodes can be altered and one can observe how these changes propagate through the network and affect other nodes. Figure 5 for example shows how altering the type of habitat from predominantly undisturbed (a) to urban (b) changes the preferred management action to chemical treatment rather than habitat management, based on the manager's prior beliefs that the RIFA colony is more likely to be monogyne than polygyne.

Figure 5   A hypothetical example showing how BBNs can be used to select the most appropriate RIFA control option: a) the network shows that habitat management is the most appropriate management option for a RIFA colony in predominately undisturbed land, whereas; b) chemical control options are more appropriate in predominately urban habitats.

(**a**)   (**b**)
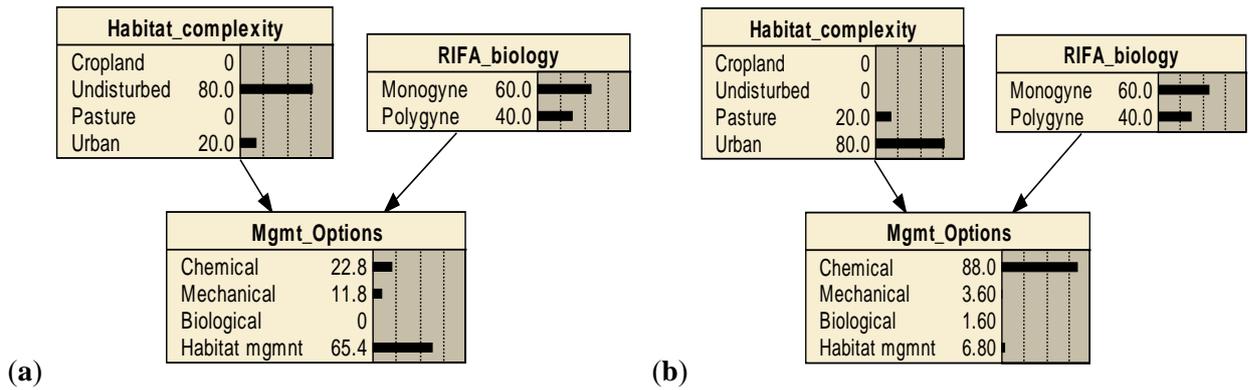
Figure 6 shows a hypothetical Decision Network (DN) based on the BBN shown in Figure 4. This DN in this example is constructed by adding a management strategy node and utility node. The management strategy node provides four potential management strategies (eradication, containment, control and mitigation). The utility node holds values (e.g., costs) for each combination of management strategy (Table 3).

Figure 6   A Bayesian Decision Network, based on the BN shown in Figure 4 showing the optimum
          management strategy for a given set of management options, habitat types and RIFA biology
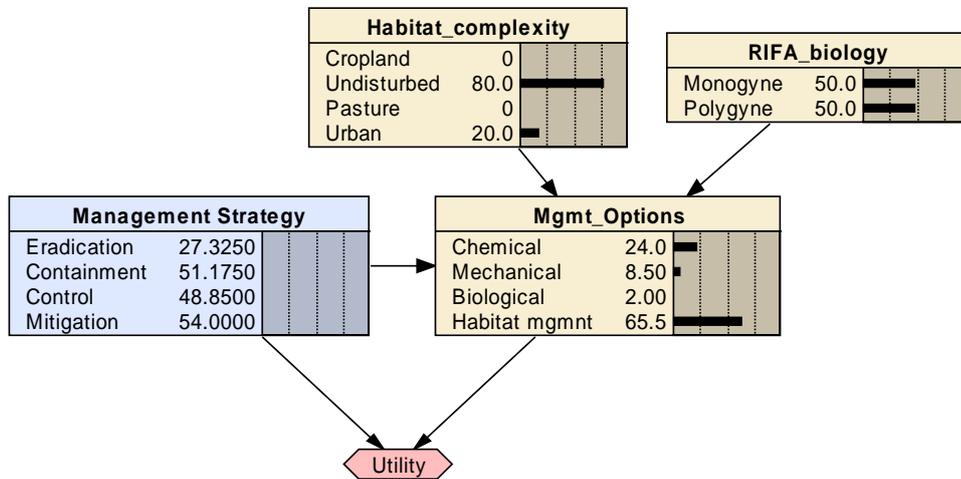
Table 3   A hypothetical utility function table for the Bayesian Decision Network shown in Figure 6
          assigning relative values to different combinations of management strategy and management
          option.

Management strategy	Management option	Utility (cost in AU$10,000)
Eradication	Chemical	90
Eradication	Mechanical	10
Eradication	Biological	80
Eradication	Habitat management	5
Containment	Chemical	50
Containment	Mechanical	65
Containment	Biological	45
Containment	Habitat management	50
Control	Chemical	70
Control	Mechanical	15
Control	Biological	65
Control	Habitat management	45
Mitigation	Chemical	35
Mitigation	Mechanical	60
Mitigation	Biological	60
Mitigation	Habitat management	60

Figure 7 shows a more complex (hypothetical) BBN that reflects a manager's beliefs (conceptual model) of the variables, and interactions between these variables, that govern the density of RIFA mounds in Australia. This network encodes the belief that RIFA density in Australia is a function of the type of habitat, RIFA biology, management option, season, other ant species and the presence of natural enemies. This type of network might typically be constructed based on the earlier examination of the factors that govern the probability of control option success, together with other empirical or scientific evidence on the natural (competitive) factors that govern RIFA density in Australia.

A sensitivity analysis (performed by Netica) can be used to determine which nodes in the RIFA BBN illustrated in Figure 7 most influence the node "RIFA Density". The results of the sensitivity analysis can be seen in Table 4. The nodes are listed from most to least influential with respect to the RIFA Density node. The most influential nodes in this BBN are the Management Option and Habitat Complexity nodes.

Figure 7   A more complex (hypothetical) belief network representing a manager's conceptual model of the key variables, and interaction between these variables, that govern the density of RIFA mounds in Australia
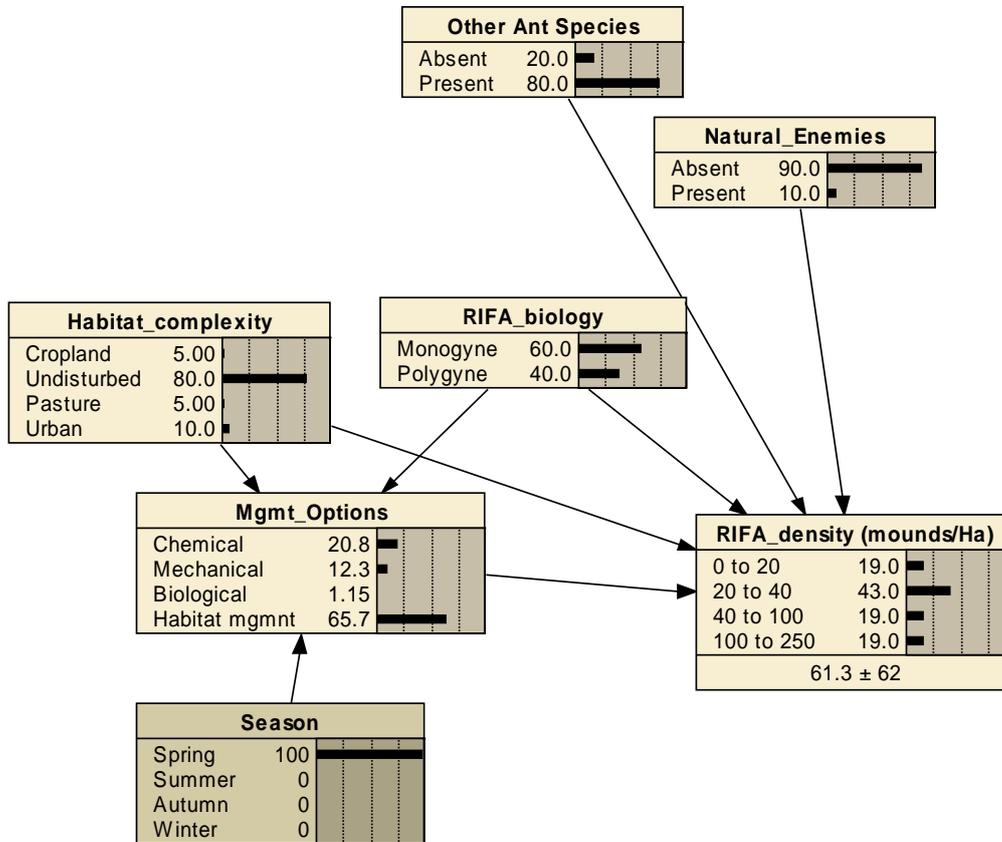
Table 4   Results of a sensitivity analysis performed for the RIFA density node of the BBN shown in Figure 7. The influence of the other nodes in the network is ranked from most to least influential. Variance reduction is the expected reduction in the variance of the output variable due to the value of an input variable.

Node	Variance reduction	Variance of Beliefs
RIFA density	3391	0.5136295
Management option	203.1	0.0454426
Habitat type	39.3	0.0085501
RIFA biology	0.9273	0.0001532
Other ant species	0.04572	0.0000074
Natural enemies	0.02491	0.0000040
Season	0	0

• **Workshop results**

The influence diagrams drafted by the participants at the workshop identified a large number of factors that determined the likelihood of successfully eradicating a RIFA outbreak in a new location, notably: the efficiency of the surveillance/detection methods, the size of the infestation, time since infestation, the environmental and land use characteristics of the location, the accuracy of a delimiting survey, accessibility of the site and treatment timing and duration. Many of these variables are reflected in the Bayes net that was prepared prior to the meeting (Figure 8).

During the workshop the BBN in Figure 8 was explored and modified in light of further information on the biology and RIFA treatment options presented to the participants at the beginning of the workshop. Two nodes were added to the BBN, representing treatment options and the effect of landscape/landuse type. Marginal and conditional probabilities were allocated to each of the nodes, such as the probability of finding the species, given it is present (=0.82 under ideal conditions), the probability of correct identification given a collection (=1), and the probability of eradication, given various treatments (ranging from 0.24 - 0.52). These data were used to populate the CPTs, together with indicative values for elements that depend on the hypothetical context.

Figure 8   Structure of Bayesian Belief Network prepared prior to the RIFA eradication workshop outlining some of the key variables that will determine the success of an eradication program
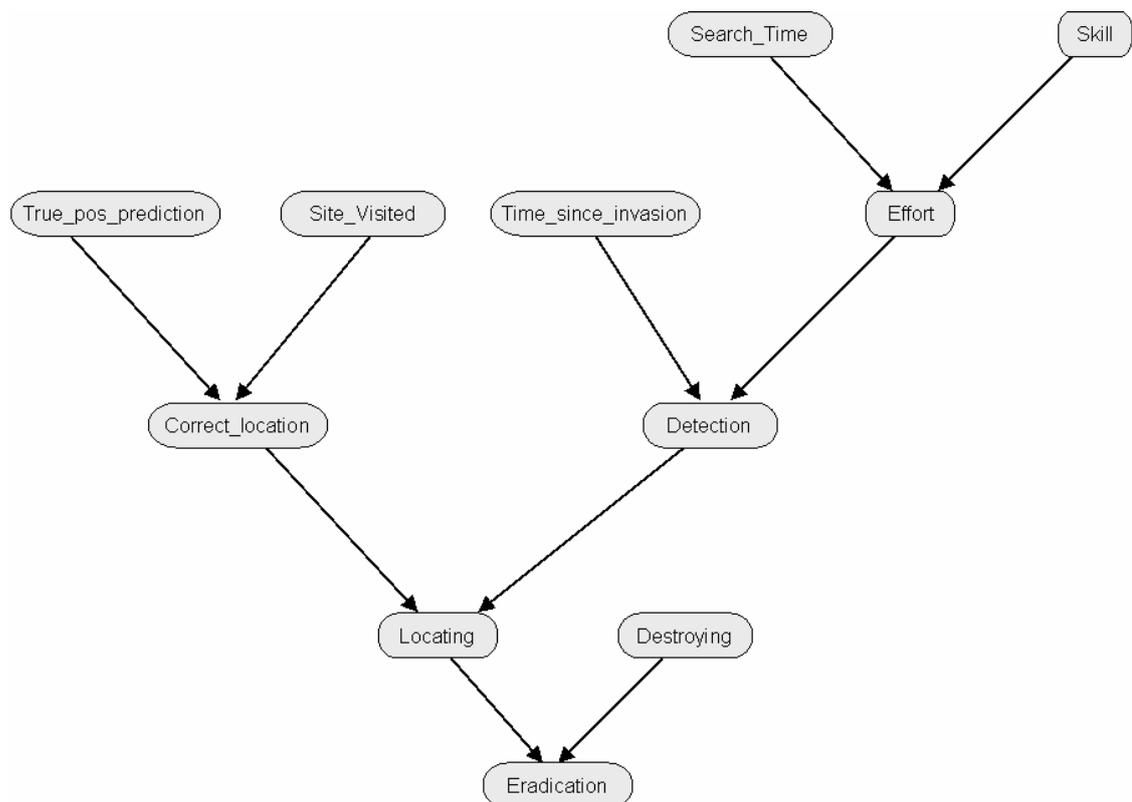
The resulting Bayes net is shown in Figure 9. This BBN suggests that eradication will be successful if the team finds the insect ('Locating') and destroys it (treatments are effective; 'Destroying'). The eradication team will find the insect if they go to the correct place ('Correct location') and are able to detect the insect when it is present ('Detection'). Detection depends on the time since invasion (RIFA are hard to find during the first few months of their residence) and on the detectability of the species, given the search methods employed and the effort expended ('Search time'). For example, the likelihood (l) that a species is absent from a site after a series of v repeat visits, given a single-visit detection probability of d and a prior estimate of the probability that the species is present of p, is given by (Wintle et al. 2005):

$$ l = \frac{p(1-d)^v}{(p(1-d)^v + (1-p))} \qquad [2] $$

The team will visit the correct location if the map of predicted occurrences directs them to the right place and if there are sufficient resources available to visit the site.

Figure 9   Bayesian Belief Network developed by the participants of the RIFA eradication workshop
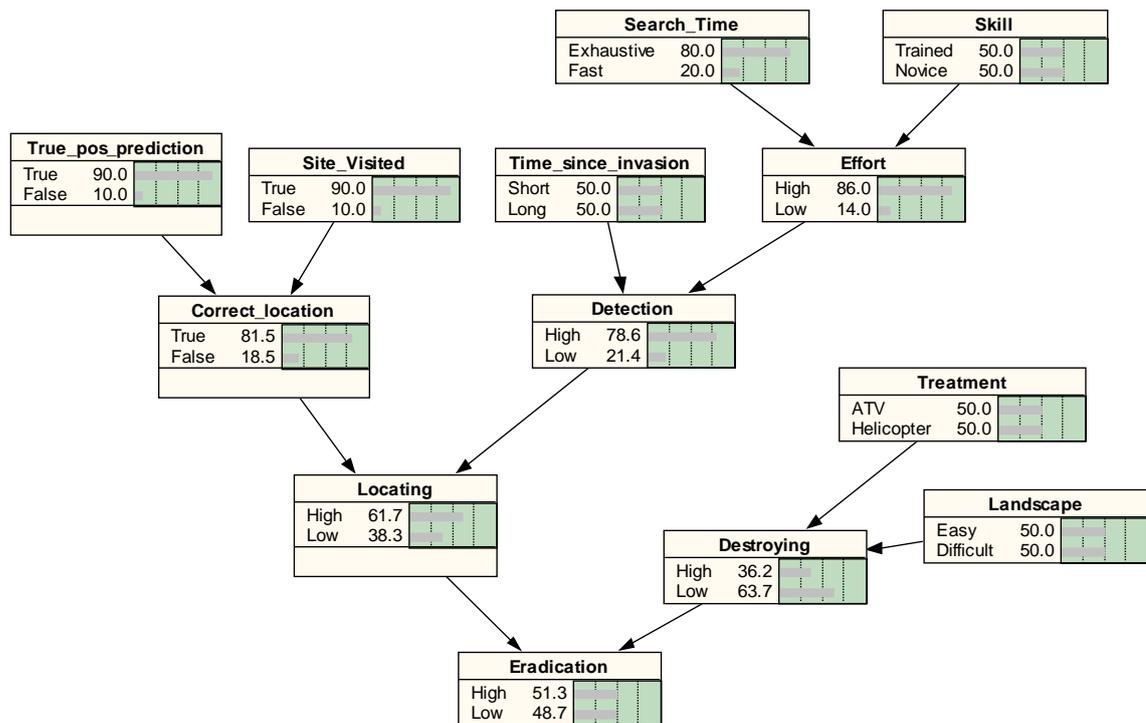
Two of the most valuable outcomes of the workshop were: a) the structured approach to thinking about the RIFA eradication problem; and, b) the development of a transparent conceptual model of the key variables and interactions between them that governed the success of an eradication attempt. This workshop highlighted the fact that the quality of the map that predicts the occurrence of the species is a critical determinant of the success of eradication attempts. It also provided a decision support framework within which the importance of training and commitment among staff could be evaluated, together with the value of information about detection functions and treatment effectiveness. The BBN developed during the workshop can

also be empirically updated using field measures of actual map performance and detection success rates in different landscape types.

The BBN shown in Figure 9 omits several potentially important factors, such as policy and coordination, containment and re-infestation. Each of these could be explored in turn and their importance evaluated. A similar BBN could be constructed to assess the importance and effectiveness of various elements in on-going surveillance programs. The network also assumes that eradication is prescribed and that governance and policy issues are resolved.

The building of the BBN prompted discussion among the participants about the effectiveness of the program, measures of its success, and triggers that would identify the need to move from a philosophy of eradication to one of control. It was clear from the discussion that there was strong consensus that success should not be measured by whether the species has been entirely eliminated or not. Australia's existing RIFA control program has not entirely eliminated RIFA but has had striking success removing the pest from large areas of suburban Brisbane. In doing so, the program has significantly improved the quality of life for the people in those areas. The program has been (roughly) 90% successful in eliminating the species. It has thereby reduced the chance of infestations to other, more remote locations, again very difficult to quantify, and has retained the option of trying to achieve 100% eradication.

The data presented to the workshop suggested that the eradication process is 'on track', in the sense that there is a downwards trend in abundance and distribution. The meeting also discussed the fact that eradication programs chase an increasingly difficult objective. As they succeed in reducing abundance and distribution, the chances of detection fall, making the last remaining sites relatively difficult to find. One of the important advantages of the BBN is that the effects of the phenomena on the probability of eradication can be explicitly explored, highlighting the requirement for very high quality predictive maps and detection functions. The program has planned further investments in these activities including improved mapping and detection activities.

- ## BIOSECURITY CASE STUDY II - *PUCCINIA PSIDII*

- ## Background

Puccinia psidii is a fungus native to South America that infects plants of the family Myrtaceae and Heteropyxidaceae. First known as guava rust, it has been introduced to Central America, Mexico, Florida, and parts of the Caribbean, where it has become a severe disease problem for eucalypt species in hardwood plantations, hence its other popular name of eucalyptus rust.

Once introduced and established, eucalyptus rust has the potential to spread rapidly. For instance in 2005 it was first observed in a commercial nursery on Oahu Island. From here it spread throughout the entire Hawaiian Island chain within a six-month period. Though it has not been detected in Australia, it is considered a serious threat to Australian forest, heath, and wet lands because of the 70 genera and roughly 1600 native tree and shrub species of the family Myrtaceae (Glen et al. 2007), many of which are of high economic and conservation value and include the genera *Callistemon* (bottlebrush), *Corymbia* and *Eucalyptus* (eucalypts), *Leptospermum* (tea tree), *Melaleuca* (paperbarks), *Osbornia* (mangrove) and *Syzygium* (lilly pillies or Australian cherries).

In preliminary susceptibility trials (with a 5% sample of Myrtaceae species), 87% of tested species were found to be susceptible to eucalyptus rust (Glen et al. 2007). Successful generation and germination of *P. psidii* spores requires specific temperature range of (roughly) 12–25°C and relatively humid conditions, and field studies suggest that rust disease incidence and severity are highly correlated with these factors (Glen et al. 2007). Tropical and temperate forest ecosystems along the east coast of Australia (Figure 10) are therefore considered to be at highest risk of infection. A key research issue identified by AGDAFF biologists was to understand how eucalyptus rust might impact native hosts and associated ecosystems.

Figure 10   Risk of *Puccinia psidii* infection in Australia; (adapted from Glen et al. 2007).
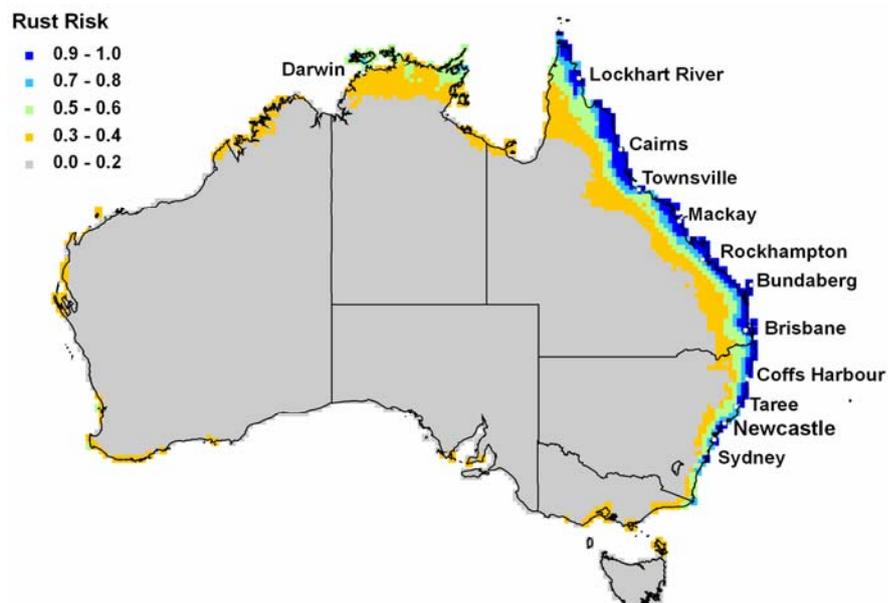
- **Methods**

A first meeting with biologists from AGDAFF was held on 1st September 2006 to briefly introduce the concepts and methods of qualitative modelling so as to provide a framework to define the general bounds of the case study. This meeting explored the known or hypothesized processes, factors and variables that govern Australian forest dynamics and eucalyptus rust infection. Initial discussions ranged broadly across multiple scales of organization including environmental physiology of rust and eucalypts, population ecology of forest plant species, and associated socioeconomic systems. By focussing on the key processes and functional aspects of the problem, the perceived structure of the system was narrowed down into a single core model that was spatially constrained to subtropical Australian eucalypt forests.

This elicitation process was repeated in three separate meetings between January 2007 and February 2007 with forest pathologists from Ensis Forest Biosecurity and Protection and Forestry Tasmania, who were kept unaware of information and core model developed in the first meeting with AGDAFF biologists. A final meeting on the 20th February included both AGDAFF and Ensis staff was used to elaborate alternative models based on different scenarios, hypotheses, and assumptions about the system's structure.

- **Results**

- **Essential features of *P. psidii* in Australian forests**

If introduced to Australia *P. psidii* is only expected to infect Myrtaceae species. From South American plantations growing Australian eucalypts, it is known that the rust causes disease primarily in young shoots, where it can cause shoot death, defoliation, and death of young trees (Glen et al. 2007). Mature foliage (>2 yrs old) is apparently unaffected, and it is thought that it will not directly kill mature trees (Ferreira 1983). Many Myrtaceae species produce two forms of shoots. Coppice shoots originate from a subsurface lignotuber and emerge after destruction of the tree limbs and trunk, as occurs in stand-replacement fires or forest harvest; epicormic shoots emerge from the trunks and branches of trees when only the leaves have been removed, as from canopy fires and out-breaks of defoliating insects (Gill 1997). It is generally accepted that coppice shoots will largely be susceptible to *P. psidii* infection (Glen et al. 2007), but there is uncertainty as to the relative susceptibility of epicormic shoots. Since these shoots occur higher in the canopy where humidity is generally lower, they may be less susceptible to rust infection.

Many Myrtaceae species are able to out-compete other native plant species in Australian forests because they are well adapted to fire: Myrtaceae regenerate quickly from coppice and epicormic shoots (Burrows 2002), and are protected from fire by thick insulating bark (McCaw et al. 1994). In the absence of fire, however, they are generally the weaker competitor, both in the understorey and overstorey (Withers and Ashton 1977, Withers 1978–1979, Williams and Gill 1995, Kirkpatrick 1997). The fire disturbance regime is therefore a key feature in Australian forest dynamics. The workshop participants identified three different fire regimes based on fire frequency and intensity. In general non-Myrtaceae species are the dominant vegetation type where fire is suppressed and Myrtaceae dominate where fire is present, but herbaceous vegetation dominates the understorey where fires are frequent (Table 5, Austin 1997).

Table 5   Relative abundance of vegetation types in temperate Australian forests under different fire

regimes.

Fire frequency	Fire intensity	Overstorey		Understorey		
		Myrtaceae	non-Myrtaceae	Myrtaceae	non-Myrtaceae	Herbaceous
none	none	low	high	low	high	low
low	high	high	low	high	low	low
high	low	high	low	low	low	high

Selection and breeding programs in Brazilian plantations have identified the possibility that *Eucalyptus* spp. can potentially develop resistance to infection from *P. psidii* (Tommerup et al. 2003); hence the potential impact of natural selection was identified as a key feature to consider in alternative models. Lastly, understorey humidity was identified as an important variable that could potentially regulate the spread of rust in forests where the fire regime suppresses, but does not totally eliminate, the growth of woody plants in the understorey.

- **Core and alternative models**

The independent elicitation process resulted in the same core model (A1 in Figure 11). This core model is based on a division of woody plants into functional guilds of Myrtaceae and non-Myrtaceae species, each with understorey and overstorey components. This division is meant to reflect general differences in fire regeneration potential and susceptibility to *P. psidii* infection. The division is imperfect however, as there is variation in the relative interdependence of fire and Myrtaceae spp. (Gill 1997), and perhaps as much as 13% of Myrtaceae species will not be susceptible to rust infection (Glen et al. 2007).

The overstorey component of non-susceptible (i.e., non-Myrtaceae) species is depicted as being able to suppress the overstorey of susceptible (i.e., Myrtaceae) species through competition for light and suppression of regeneration, while competition between the understorey variables is reciprocal and mediated by allelopathy, seed predation, drought resistance, and shading (Withers 1978a, 1978b, 1979b; Kirkpatrick 1997). It was generally considered that in the absence of fire the understorey component of the non-susceptible species would be superior competitors. Non-woody, or herbaceous vegetation, is depicted as being suppressed by both susceptible and non-susceptible species of woody plants. From the core model a set of alternative models was developed based on the absence or presence of *P. psidii* under three different fire regimes (Figure 11 and Figure 12), including a "no-fire" regime where fire does not occur or has been effectively suppressed across the landscape, a regime with infrequent but intense fires, and one where fires were frequent and of low intensity. Additional models encompass uncertainty in the susceptibility of epicormic shoots to rust infection, and the influence of natural selection and understorey humidity on rust virulence.

- **Models A1, B1 & C1: no rust under three different fire regimes**

Models A1, B1, and C1 represent the current rust-free condition of Australian temperate forests.

Model A1 represents the case where fire does not occur on the landscape, and its dynamics are determined primarily by the competitive relationship between Myrtaceae (variables MO and MU) and non-Myrtaceae (variables NO and NU). Here non-Myrtaceae species are known to be the stronger competitor, such that $a_{4,2} < a_{2,4}$. Under this condition, the equilibrium abundance of non-Myrtaceae are expected to be greater than Myrtaceae spp, which is consistent with Table 5. This condition is also key in determining the stability properties of the model (Table 6). If Myrtaceae and non-Myrtaceae species were equally strong competitors, such that $a_{4,2} \approx a_{2,4}$ and self-regulation was relatively week, such that $a_{4,2}a_{2,4} > a_{2,2}a_{4,4}$, then the system would be unstable.

In model A1 the positive product of competitive interactions between the understorey vegetation (MU and NU), $a_{4,2}a_{2,4}$, creates a positive feedback cycle that supports the existence of two alternative stable states. The effect of this feedback is evident in the adjoint matrix for model A1 (Table 7). Here a positive input to either of the understorey variables MU or NU leads to opposite response on the other and its respective overstorey component. For instance, a positive input to MU, read down the second column of A1's adjoint matrix, leads to more of MO and less of NU and NO. In the context of temperate forests, these alternative states are expressed as coarse scale heterogeneity in the composition of forest stands, where there is patchiness in conditions or disturbance events that favour one type of vegetation over another.

Model B1 includes the influence of an infrequent-intense fire regime. In this scenario fire creates a disturbance regime that stimulates the production of epicormic and coppice growth. Epicormic growth, however, is a rapid transitory phase that has no influence on the feedback properties of this model. It only becomes important if it forms feedback cycles with other variables (see Models B3 and B5). The influence of fire on coppice shoot growth favours understorey Myrtaceae, which in turn suppresses recruitment opportunities for non-Myrtaceae in both the understorey and overstorey, the latter affording a greater potential for coppice growth in the presence of fire. These effects constitute two positive feedback cycles: 1) Cop→MU→MO→Cop; and 2) Cop→MU⎯•NU→NO⎯• MO→Cop), that dominate the stability properties of the system (Table 6). In addition to the same conditions for stability in model A1, stability in this model is partially ensured by the condition that positive feedback from coppice formation will always be less than the product of the self-effects in the Myrtaceae variables (i.e., $a_{2,7} a_{7,1}a_{1,2} < a_{1,1}a_{2,2}a_{7,7}$).

The effect of a press perturbation to fire in this system can be investigated by reading down the sixth column of model B1's adjoint matrix (Table 7) - the model predicts that all components of Myrtaceae growth will increase (i.e., have positive entries within the sixth column of the adjoint matrix) and that all other vegetation variables will decline in their abundance (i.e., have negative adjoint matrix elements). All of these predictions are supported by relatively high probabilities for sign determinacy. Moreover, these predictions are in accord with the relative abundances described for Australian temperate forests in Table 5, which generally suggest that only Myrtaceae species will have high relative abundances where fires are infrequent and intense.

Figure 11 Sign digraph models of temperate Australian forests in the presence or absence of disease from the rust *Puccinia psidii*, under three different fire regimes, the influence of coppice and epicormic shoot growth in eucalypt species, understorey humidity, and natural selection for rust-resistance. Cop: coppice shoot growth, Epi: epicormic shoot growth, H: herbaceous vegetation, Hum: understorey humidity, N: non-Myrtaceae species, O: overstorey vegetation, M: Myrtaceae species, SD: selection differential, U: understorey vegetation.

Model A1: no-fire regime, no rust
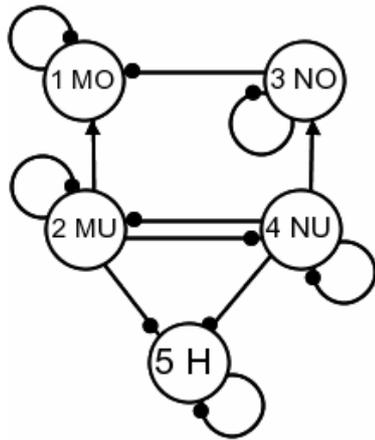
Model A2: no-fire regime, with rust
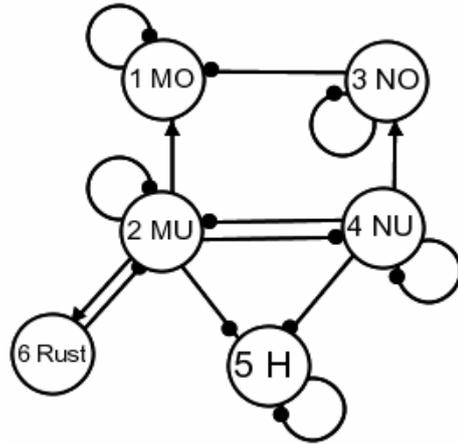
Model B1: infrequent-intense fire, no rust and coppice shoot growth
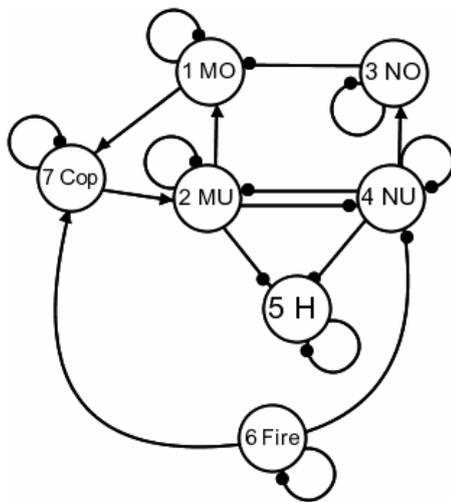
Model B2: infrequent-intense fire, with rust and coppice shoot growth
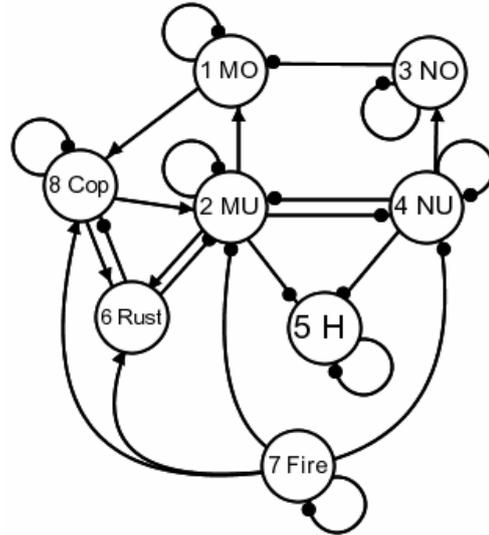
Figure 12 Continuation of Figure 11

Model B3: infrequent-intense fire, with rust, coppice and epicormic shoot growth
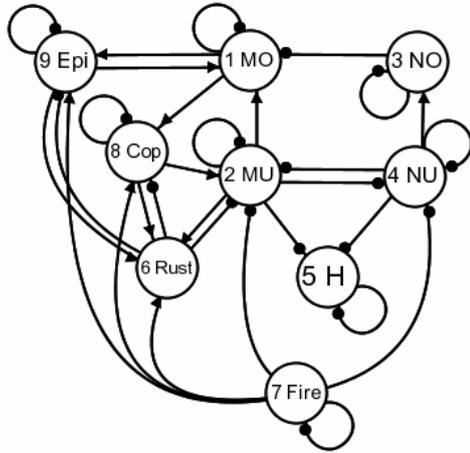
Model B4: infrequent-intense fire with rust, coppice shoot growth and natural selection
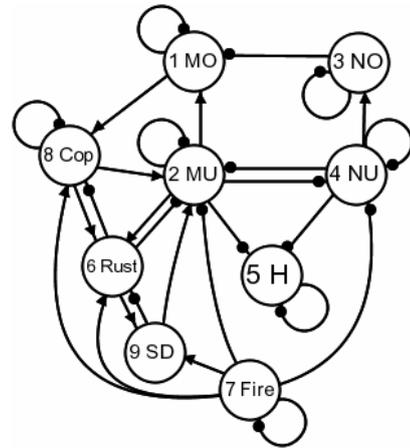
Mode B5: infrequent-intense fire with rust, coppice, epicormic shoot growth and natural selection
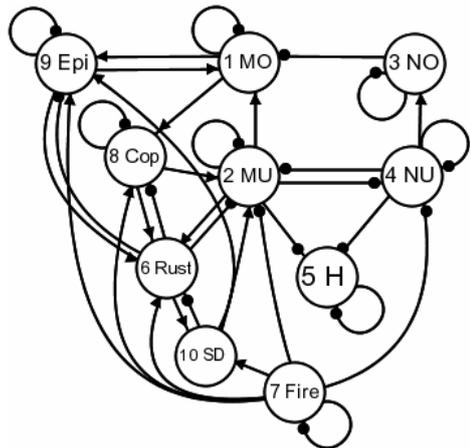
Model C1: frequent low-intensity fire, no rust
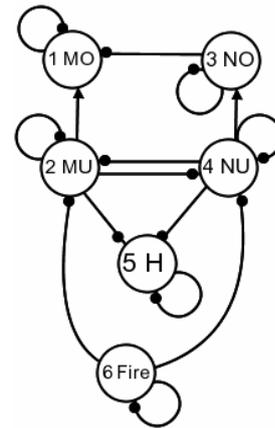
Model C2: frequent low-intensity fire with rust
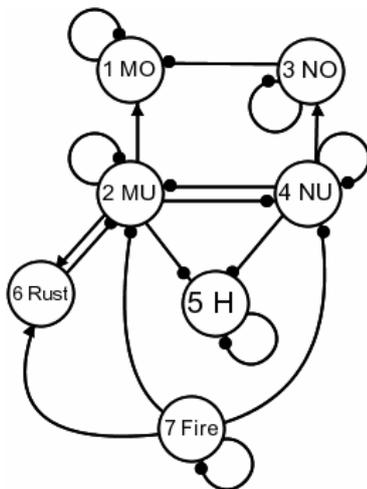
Model C3: frequent low-intensity fire with rust and understorey humidity variable
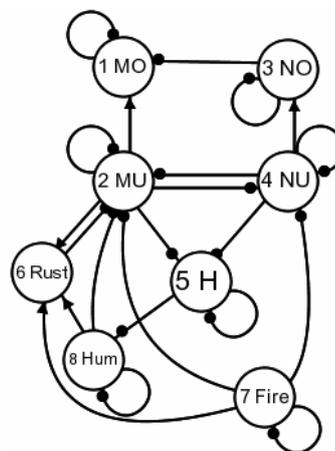
Table 6   Stability properties of sign digraph models of temperate Australian forests (Figure 11 and 12). See Appendix A for explanation of stability metrics; Cop: coppice shoots, Epi: epicormic shoots, H: herbaceous vegetation, Hum: humidity in understorey, M: Myrtaceae species, N: non-Myrtaceae species, O: overstorey vegetation, SD: selection differential, U: understorey vegetation.

Model	Stability class & metric	Comments
A1	Class I $wF_n = 0$	Stability depends on density-dependent self-regulation in understorey vegetation being greater than intraspecific competition, such that $a_{2,2}a_{4,4} > a_{2,4}a_{4,2}$. This condition is reasonable, as it is presumed $a_{4,2}$ is relatively weak and $a_{4,2} < a_{2,4}$.
A2	Class II $w\Delta^C_{n-1} = 7.2$	Relative to model A1, system dominated by negative feedback cycles, but stability now depends on strength of lower level feedback being greater than higher level feedback, such that $a_{2,2}(a_{4,4}^2 + a_{2,2}a_{4,4} + a_{2,6}a_{6,2}) > a_{2,4}a_{4,2}(a_{2,2} + a_{4,4})$.
B1	Class I $wF_n = 0.5$	System dominated by positive feedback driven by links associated with coppice shoots, but partially balanced by self-regulation in the MO-Cop-MU subsystem.
B2	Class II $w\Delta^C_{n-1} = 48$	Relative to model B1, system is stabilized by negative feedback in Cop-MU-Rust subsystem, and in its feedback with whole system.
B3	Class I $wF_n = -0.24$	Relative to model B1, and similar to model B2, system is stabilized by negative feedbacks that include links between epicormic shoots and rust, and additional links to whole system. As in B1, positive feedback from Epi and MO subsystem balanced by self-regulation.
B4	Class I $wF_n = 0.71$	Low potential for stability; system dominated by positive feedback generated by links with selection differential (SD).
B5	Class I $wF_n = 0.26$	Low potential for stability; system dominated by positive feedback generated by links with selection differential (SD).
C1	Class I $wF_n = 0$	Stability conditions same as model A1.
C2	Class II $w\Delta^C_{n-1} = 48$	Relative to model C1, system stabilized by addition of pairwise links between Rust and MU variables and thus relative potential for stability is higher.
C3	Class I $wF_n = -0.33$	Relative to model C2, potential for stability diminished by positive feedback from MU-NU-H-Hum-Rust subsystem, but potential stability is higher than model C1.

Table 7 Prediction matrices for alternative models (Figure 7) of temperate Australian forests; Cop: coppice shoot growth, Epi: epicormic shoot growth, H: herbaceous vegetation, Hum: understorey humidity, N: non-Myrtaceae species, O: overstorey vegetation, M: Myrtaceae species, SD: selection differential, U: understorey vegetation. Dashed lines highlight press perturbations discussed in the report

Model	Adj($-^{\circ}$A)	Probability sign adj($-^{\circ}$A) correct
A1 1: MO 2: MU 3: NO 4: NU 5: H	$\begin{bmatrix} 0 & 2 & 0 & -2 & 0 \\ 0 & 1 & 0 & -1 & 0 \\ 0 & -1 & 0 & 1 & 0 \\ 0 & -1 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$	$\begin{bmatrix} 0 & 1 & 0 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 0 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 \\ 1 & 0 & 1 & 0 & 0 \end{bmatrix}$
A2 1: MO 2: MU 3: NO 4: NU 5: H 6: Rust	$\begin{bmatrix} 1 & 0 & -1 & -1 & 0 & -2 \\ 0 & 0 & 0 & 0 & 0 & -1 \\ 0 & 0 & 1 & 1 & 0 & 1 \\ 0 & 0 & 0 & 1 & 0 & 1 \\ 0 & 0 & 0 & -1 & 1 & 0 \\ 0 & 1 & 0 & -1 & 0 & 0 \end{bmatrix}$	$\begin{bmatrix} 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 & 0 \\ 1 & 1 & 1 & 1 & 1 & 0 \end{bmatrix}$
B1 1: MO 2: MU 3: NO 4: NU 5: H 6: Fire 7: Cop	$\begin{bmatrix} 0 & 2 & 0 & -2 & 0 & 4 & 2 \\ 1 & 1 & -1 & -2 & 0 & 3 & 1 \\ -1 & -1 & -1 & 0 & 0 & -1 & -1 \\ -1 & -1 & 1 & 0 & 0 & -1 & -1 \\ 0 & 0 & 0 & 2 & -2 & -2 & 0 \\ 0 & 0 & 0 & 0 & 0 & -2 & 0 \\ 0 & 2 & 0 & -2 & 0 & 2 & 0 \end{bmatrix}$	$\begin{bmatrix} 0 & 1 & 0 & 1 & 1 & 1 & 1 \\ 1 & 1 & 1 & 1 & 1 & 1 & 1 \\ 1 & 1 & 0.77 & 0 & 1 & 0.77 & 1 \\ 1 & 1 & 1 & 0 & 1 & 0.77 & 1 \\ 0 & 0 & 0 & 0.87 & 0.87 & 0.79 & 0 \\ 1 & 1 & 1 & 1 & 1 & 0.87 & 1 \\ 0 & 1 & 0 & 1 & 1 & 0.87 & 0 \end{bmatrix}$
B2 1: MO 2: MU 3: NO 4: NU 5: H 6: Rust 7: Fire 8: Cop	$\begin{bmatrix} 2 & 2 & -2 & -4 & 0 & -4 & -4 & -2 \\ -1 & 1 & 1 & 0 & 0 & -2 & -4 & -1 \\ 1 & -1 & 3 & 4 & 0 & 2 & 0 & 1 \\ 1 & -1 & -1 & 4 & 0 & 2 & 0 & 1 \\ 0 & 0 & 0 & -4 & 4 & 0 & 4 & 0 \\ 1 & 3 & -1 & -4 & 0 & -2 & 0 & 1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 4 & 0 \\ 1 & -1 & -1 & 0 & 0 & -2 & 0 & 1 \end{bmatrix}$	$\begin{bmatrix} 0.87 & 1 & 0.87 & 1 & 1 & 1 & 0.79 & 1 \\ 1 & 1 & 1 & 0 & 1 & 1 & 0.92 & 1 \\ 1 & 1 & 0.90 & 1 & 1 & 1 & 0 & 1 \\ 1 & 1 & 1 & 1 & 1 & 1 & 0 & 1 \\ 0 & 0 & 0 & 0.92 & 0.92 & 0 & 0.75 & 0 \\ 0.77 & 1 & 0.77 & 1 & 1 & 0.87 & 0 & 0.77 \\ 1 & 1 & 1 & 1 & 1 & 1 & 0.92 & 1 \\ 1 & 1 & 1 & 0 & 1 & 0.87 & 0 & 1 \end{bmatrix}$
B3 1: MO 2: MU 3: NO 4: NU 5: H 6: Rust 7: Fire 8: Cop 9: Epi	$\begin{bmatrix} 2 & 3 & -2 & -5 & 0 & -4 & -5 & -1 & -2 \\ -2 & 2 & 2 & 0 & 0 & -1 & -5 & 1 & -3 \\ 2 & -2 & 3 & 5 & 0 & 1 & 0 & -1 & 3 \\ 2 & -2 & -2 & 5 & 0 & 1 & 0 & -1 & 3 \\ 0 & 0 & 0 & -5 & 5 & 0 & 5 & 0 & 0 \\ 1 & 4 & -1 & -5 & 0 & -2 & 0 & 2 & -1 \\ 0 & 0 & 0 & 0 & 0 & 0 & 5 & 0 & 0 \\ 1 & -1 & -1 & 0 & 0 & -2 & 0 & 2 & -1 \\ 1 & -1 & -1 & 0 & 0 & -2 & 0 & -3 & 4 \end{bmatrix}$	$\begin{bmatrix} 0.79 & 0.90 & 0.79 & 0.94 & 1 & 0.92 & 0.67 & 0.63 & 0.72 \\ 0.87 & 0.87 & 0.87 & 0 & 1 & 0.68 & 0.72 & 0.77 & 1 \\ 0.87 & 0.87 & 0.68 & 0.82 & 1 & 0.68 & 0 & 0.77 & 1 \\ 0.87 & 0.87 & 0.87 & 0.82 & 1 & 0.68 & 0 & 0.77 & 1 \\ 0 & 0 & 0 & 0.73 & 0.73 & 0 & 0.63 & 0 & 0 \\ 0.68 & 0.92 & 0.68 & 0.94 & 1 & 0.79 & 0 & 0.72 & 0.63 \\ 1 & 1 & 1 & 1 & 1 & 1 & 0.73 & 1 & 1 \\ 0.68 & 0.63 & 0.68 & 0 & 1 & 0.72 & 0 & 0.79 & 0.68 \\ 0.63 & 0.68 & 0.63 & 0 & 1 & 0.72 & 0 & 0.90 & 0.92 \end{bmatrix}$

Table 8   continuation of Table 7

Model	Adj(−°A)	Probability sign adj(−°A) correct

B4

1: MO
2: NU
3: NO
4: NU
5: H
6: Rust
7: Fire
8: Cop
9: SD

Adj(−°A):
```
-1   2   1  -1   0   2 | 11 |  4   6
 2   1  -2  -3   0   1 |  8 |  2   3
-2  -1  -3  -2   0  -1 | -3 | -2  -3
-2  -1   2  -2   0  -1 | -3 | -2  -3
 0   0   0   5  -5   0 | -5 |  0   0
 0   0   0   0   0   0 |  5 |  0   5
 0   0   0   0   0   0 | -5 |  0   0
-1   2   1  -1   0   2 |  1 | -1   1
 1   3  -1  -4   0  -2 |  4 |  1   4
```

Probability sign adj(−°A) correct:
```
0.77   1   0.77  0.77   1   1 | 0.94 |  1     1
 1     1    1     1     1   1 | 0.96 |  1     1
 1     1   0.90  0.87   1   1 | 0.73 |  1     1
 1     1    1    0.87   1   1 | 0.73 |  1     1
 0     0    0    0.94  0.94  0 | 0.73 |  0     0
 1     1    1     1     1   1 | 0.94 |  1    0.94
 1     1    1     1     1   1 | 0.94 |  1     1
0.77   1   0.77  0.77   1   1 | 0.57 | 0.77  0.68
0.77   1   0.77   1     1  0.87| 0.70 | 0.77  0.92
```

B5

1: MO
2: MU
3: NO
4: NU
5: H
6: Rust
7: Fire
8: Cop
9: Epi
10: SD

Adj(−°A):
```
-1   1   1   0   0   2 | 10 |  3   1   5
 2  -2  -2   0   0   1 |  5 | -1   3   0
-2   2  -3  -5   0  -1 |  0 |  1  -3   0
-2   2   2  -5   0  -1 |  0 |  1  -3   0
 0   0   0   5  -5   0 | -5 |  0   0   0
 0   0   0   0   0   0 |  5 |  0   0   5
 0   0   0   0   0   0 | -5 |  0   0   0
-1   1   1   0   0   2 |  0 | -2   1   0
 0   5   0  -5   0   0 |  5 |  5  -5   5
 1   4  -1  -5   0  -2 |  5 |  2  -1   5
```

Probability sign adj(−°A) correct:
```
0.68  0.68  0.68   0     1   0.87 | 0.75 | 0.79  0.68  0.75
0.87  0.87  0.87   0     1   0.77 | 0.66 | 0.68   1     0
0.87  0.87  0.69  0.86   1   0.77 |  0   | 0.68   1     0
0.87  0.87  0.87  0.86   1   0.77 |  0   | 0.68   1     0
 0     0     0    0.75  0.75  0   | 0.60 |  0     0     0
 1     1     1     1     1    1   | 0.75 |  1     1    0.75
 1     1     1     1     1    1   | 0.75 |  1     1     1
0.68  0.68  0.68   0     1   0.87 |  0   | 0.69  0.68   0
 0     1     0    0.94   1    0   | 0.63 | 0.94  0.94  0.75
0.68  0.92  0.68  0.94   1   0.79 | 0.62 | 0.72  0.63  0.73
```

C1

1: MO
2: MU
3: NO
4: NU
5: H
6: Fire

Adj(−°A):
```
0   2   0  -2   0 | 0
0   1   0  -1   0 | 0
0  -1   0   1   0 | 0
0  -1   0   1   0 | 0
0   0   0   0   0 | 0
0   0   0   0   0 | 0
```

Probability sign adj(−°A) correct:
```
0   1   0   1   1 | 0
1   1   1   1   1 | 0
1   1   0   1   1 | 0
1   1   1   1   1 | 0
1   0   1   0   0 | 0
1   1   1   1   1 | 0
```

C2

1: MO
2: MU
3: NO
4: NU
5: H
6: Rust
7: Fire

Adj(−°A):
```
1   0  -1  -1   0  -2 | -1
0   0   0   0   0  -1 | -1
0   0   1   1   0   1 |  0
0   0   0   1   0   1 |  0
0   0   0  -1   1   0 |  1
0   1   0  -1   0   0 |  0
0   0   0   0   0   0 |  1
```

Probability sign adj(−°A) correct:
```
1   1   1   1   1   1 | 0.77
1   1   1   1   1   1 |  1
1   1   1   1   1   1 |  0
1   1   1   1   1   1 |  0
1   1   1   1   1   0 | 0.77
1   1   1   1   1   0 |  0
1   1   1   1   1   1 |  1
```

C3

1: MO
2: MU
3: NO
4: NU
5: H
6: Rust
7: Fire
8:Hum

Adj(−°A):
```
1   0  -1  -3   2  -2 |  1 | -2
0   0   0  -1   1  -1 |  0 | -1
0   0   1   2  -1   1 | -1 |  1
0   0   0   2  -1   1 | -1 |  1
0   0   0  -1   1   0 |  1 |  0
0   1   0  -2   1   0 |  1 | -1
0   0   0   0   0   0 |  1 |  0
0   0   0   1  -1   0 | -1 |  1
```

Probability sign adj(−°A) correct:
```
0.77   1   0.77   1     1    1 | 0.68 |  1
 1     1    1     1     1    1 |  0   |  1
 1     1   0.77   1     1    1 | 0.77 |  1
 1     1    1     1     1    1 | 0.77 |  1
 1     1    1     1     1    0 | 0.77 |  0
 1    0.77  1    0.87  0.77  0 | 0.58 | 0.77
 1     1    1     1     1    1 | 0.77 |  1
 1     1    1     1     1    0 | 0.77 |  1
```

Model C1 depicts frequent low-intensity fires as having a negative effect on both the susceptible (MU) and non-susceptible (NU) groups of understorey woody vegetation. The stability properties of this model are identical to that of model A1. Here fire intensity is too low to cause crown scorch that results in coppice growth, so there is no clear regeneration advantage afforded to Myrtaceae species. Instead frequent fires limit seedling survival in both groups of woody vegetation. In this model, an input to fire yields qualitative predictions with an equal number of positive and negative feedback cycles contributing to each response, such that for an input to fire, all adjoint matrix elements and probabilities for sign determinacy are zero (Table 7). Adjoint matrix elements that are zero indicate an ambiguous response – i.e., the response may be positive or negative depending on the (unknown) magnitude of the interaction coefficients (a_{ij}) in the various feedback cycles. In this case, however, these ambiguities can be addressed, at least in part, through the previously discussed condition of $a_{4,2} < a_{2,4}$. If this condition is maintained throughout the symbolic arguments of the adjoint matrix, then the sign of response elements (sign adj($-°A$)$_{i,6}$) is [+, ?, –, –, +, +]^T. This corresponds to an increase in overstorey Myrtaceae and herbaceous vegetation, a decline in non-Myrtaceae species in the overstorey and understorey, while the impact to understorey Myrtaceae remains ambiguous. Again these predictions are consistent with the relative abundances described in Table 5.

- **Model A2: rust present in a no-fire regime**

Model A2, as well as all subsequent models discussed below, explores the consequence of *P. psidii* becoming established in subtropical eucalypt forests. As *P. psidii* is known to only infect Myrtaceae species, its abundance depends entirely on susceptible Myrtaceae, and thus its variable is not self-regulated. Relative to model A1, the addition of the pairwise parasitism links (Figure 11) adds negative system feedback that balances the potential for positive overall feedback in model A1. Stability in this system depends on the strength of lower level feedback being greater than higher level feedback (Table 6). As in previous models, stability is supported by the condition $a_{4,2} < a_{2,4}$, but additionally in this model by the condition that the product of the links associated with *P. psidii* virulence ($a_{6,2}a_{2,6}$) is relatively strong. Taken together, both of these conditions support the common-sense result that, relative to model A1, Myrtaceae species would persist at reduced equilibrium abundances. These results are corroborated in Table 7, where an input (increase) to the rust variable (column 6) results in an increase in non-Myrtaceae species and a decrease in Myrtaceae species.

- **Models B2 and B3: infrequent-intense fire with rust**

Including *P. psidii* in models B2 and B3 adds multiple sets of pairwise links with understorey Myrtaceae, coppice growth and epicormic growth. These links provide a substantial increase in the stability of the system in terms of negative feedbacks (Table 6). In both of these models, fire enhances the two-way parasitic interaction between rust and the Myrtaceae understorey. This effectively creates a negative direct effect between fire and the Myrtaceae understorey ($a_{2,7}$), and a positive direct effect on rust from fire ($a_{6,7}$). The combined effect of these new links reverses what was, in model B1, a positive effect of fire on Myrtaceae species. Hence, an input to fire in models B2 or B3 will likely decrease Myrtaceae in both the forest overstorey and understorey, though the response of non-Myrtaceae woody vegetation is ambiguous, with an increase or decrease equally likely (Table 7). Furthermore, an input to fire suppresses herbaceous vegetation in model B1, but in models B2 and B3 an increase is the more probable response.

- **Model C2: frequent low-intensity fire with rust**

Introduction of *P. psidii* to a low-intensity fire regime in model C2 creates essentially the same dynamics described for models B2 and B3 above. The pairwise links associated with rust act to stabilize the system, and in the presence of rust an input to fire will likely lead to a decrease in the abundance of Myrtaceae vegetation and an increase in herbaceous vegetation, while the response of non-Myrtaceae variables and rust is ambiguous.

- **Models B4 and B5: influence of natural selection**

Models B4 and B5 consider the influence of rust resistant genotypes in populations of Myrtaceae species undergoing natural selection. Natural selection is regulated by a system variable called the *selection differential*, which is defined as the difference between the mean of a trait for parents that will survive to produce the next generation and the mean of the whole population. The trait under selection is the relative susceptibility of Myrtaceae species to rust disease and the magnitude of the selection differential variable is controlled by variables that determine Myrtaceae mortality in the presence of rust.

The selection differential variable was added to models in the infrequent-intense fire regime because of the relatively high rate of turnover in the overstorey from stand-replacement fires. While natural selection could also operate in the other fire regimes, it would do so at a much lower rate. It is therefore included in models B4 and B5 as a near-term contrast to the other models. The links associated with the selection differential variable creates an overwhelming amount of positive feedback, and both models have an exceedingly low potential for stability (Table 6). This disequilibrium, however, is consistent with how natural selection would be expected to operate in nature, and the spread of a rust resistant genotype throughout populations of Myrtaceae would provide a continual shift in the equilibrium abundances of the system as long as the selection differential variable is greater than zero. We can infer the direction of change due to natural selection by feedbacks associated with an input to fire (Table 7). In model B4 an input to fire causes an increase in rust and Myrtaceae vegetation and a decrease in all other types of vegetation. In model B5, predictions are the same for Myrtaceae and herbaceous vegetation, however the prediction for non-Myrtaceae woody vegetation is ambiguous.

- **Model C3: influence of understorey humidity**

This final model considers the influence of understorey vegetation on the microclimate of subtropical eucalypt forests, where suppression of understorey woody vegetation reduces humidity near the ground, thereby moderating rust virulence. In this model the level of the herbaceous vegetation is inversely proportional to the sum of the two types of woody vegetation, and thus high levels of herbaceous vegetation coincides with reduced understorey humidity. The relevance of this model depends on there being an intermediate level of woody vegetation growth coinciding with reduced humidity and rust virulence. If the fire regime effectively removes all woody vegetation in the understory, then this would, of course, obviate any benefits to understory Myrtaceae. The potential stability of this model is less than that of model C2 due to the positive feedback in the MU-NU-H-Hum-Rust subsystem (Figure 11 and Table 6). In this system an input to fire acts to increase rust, overstorey Myrtaceae and decrease non-Myrtaceae woody vegetation and herbaceous vegetation; the response of understorey Myrtaceae, however, is ambiguous. These predictions are similar to those interpreted for model

C1 above (given condition $a_{4,2} < a_{2,4}$), though with higher levels of sign determinacy.

• CONCLUSIONS AND DISCUSSION

Virtually all international biosecurity provisions emphasise the importance of scientifically sound risk assessment. The 1994 agreement on Sanitary and Phytosanitary Measures (the "SPS Agreement"), for example, stresses that measures to prevent the spread of plant, animal, or other disease agents must be based on a *scientific* assessment of the risks to human, animal or plant health. This requirement for scientifically sound assessments is reflected in Australia's national biosecurity provisions.

To be scientifically sound a risk assessment must be transparent, repeatable and make predictions that can be experimentally and/or statistically tested. The most important features of the two methods described in this report, Bayesian belief networks and qualitative modelling, is that they satisfy all of these criteria and can be implemented in data poor applications. SDGs and BBNs can be readily constructed based on expert and or stakeholder opinion. Furthermore they are a natural means to: a) provide prior prediction of the qualitative behaviour of a system; and, b) to explore the consequence of competing hypothesis of how a system is constructed, thus reflecting uncertainty in model structure. These techniques therefore provide a demonstrably scientific foundation to a risk assessment, and can be used to complement and strengthen existing methods of import risk assessment.

Bayesian Belief Networks (BBNs) are an increasingly popular method for modelling uncertain and complex domains such as ecosystems and environmental management (Uusitalo, 2007). Cain (2001) outlines the utility of Bayesian networks when incorporating the effects of uncertainty in complex natural resource management problems as follows:

"…*decision makers can balance the desirability of an outcome against the chance that the management option selected may fail to achieve it. This facility is particularly important for environmental management where the complexity of the natural world means that it is rarely possible to predict the exact impact of any management intervention. In an uncertain world, Bayesian networks allow users to estimate the chance that a management intervention will have a particular effect and then investigate the consequences of their uncertainty.*"

The RIFA case study described here demonstrates how BBNs can be used to identify the key variables that are thought to govern the success of an eradication campaign, and combine different sources of information – in this case literature and expert opinion – into a statistically coherent whole. The resulting network highlighted the importance of correctly predicting the location of RIFA nests particularly in the latter stages of eradication. Moreover the workshop process of building the network with a large number of stakeholders provided a very effective vehicle for information exchange and consensus building.

Accommodating realistically complex spatial and temporal dynamics, including feedback, within the acyclic structure of a BBN is possible but it is a laborious, data intensive and time consuming process. This is perhaps the most significant disadvantage of a BBN. BBNs, however, are not unusual in this respect - complex spatial and temporal dynamics pose significant hurdles to all risk assessment methods and are often ignored because it is extremely difficult to adequately parameterize these processes, particularly in data-poor situations. Realistically complex level of feedback however can be readily analysed qualitatively – as demonstrated in the Eucalyptus rust case study developed here.

The Eucalyptus rust case study demonstrates that qualitative modelling offers a methodology to handle knowledge (or model structure) uncertainty and can be used to effectively structure ambiguous knowledge into meaningful conceptual models than can be used to underpin more quantitative tools of risk analysis and assessment. In this case study we developed an array of alternative qualitative models that attempt to account for the essential dynamics of subtropical eucalypt forest ecosystems. The same core model was elicited from two separate groups of experts, and while it is a highly simplified abstraction of how a forest ecosystem might behave, its alternative elaborations nonetheless emulated known fire-disturbance dynamics of the rust-free ecosystem. Furthermore, the workshop process used to develop these models, with a range of stakeholders, once again provided a good vehicle for consensus building.

Competitive interactions emerged as a key feature of system structure, and accounting for how these interactions affect system stability and perturbation response provides a means to more deeply understand the potential impact of *P. psidii* on subtropical eucalypt forest ecosystems. Similarly, knowing how links between variables change under different fire regimes is key to understanding how the balance of competitors might shift in models with and without rust. In general, our results support the concern that *P. psidii* will likely have a negative impact on Myrtaceae species in Australian forests, and this obvious, if not trivial, result was invariant across all fire regimes, and assumptions about susceptibility of different forms of shoot growth. Our analysis supports the hypothesis that natural selection for rust resistance might progress most rapidly in an infrequent-intense fire regime. An important result of this work is that a frequent low-intensity fire regime can potentially mitigate the effects of *Eucalyptus* rust through reduced understorey humidity, and suggests critical research to investigate the strength of the influence of understorey woody vegetation on near-ground humidity.

The advantages of qualitative models – transparent, rapid, qualitative, yet rigorous, analysis – are gained by sacrificing information on the precision and magnitude of the interactions between variables in the model. In this case study developed here, the qualitative predictions of the three core models appear to be consistent with the known dynamics of Australian subtropical eucalypt forests. The case study does not, however, identify any of the subsequent seven models as being more or less likely than any other. This is an important disadvantage of qualitative modelling in general. It is important to emphasise that qualitative models are not designed to replace existing methods of biosecurity risk assessment, but rather to complement and augment these methods, particularly in the early problem formulation stage of an assessment.

The control and management of pests and diseases are implemented in a policy arena composed of laws, regulations, private and public organizations, government agencies, industry, interest groups and private consumers (Dahlsten and Garcia 1989). This dictates the need for a decision support tool that is communicable to a wide variety of stakeholders, can meaningfully combine qualitative and quantitative information, is easy to use and yet sophisticated and robust enough to explicitly manage real world uncertainties. The results of this project confirm that Bayesian Belief Networks and qualitative models can process various, potentially ambiguous, sources of data into transparent and coherent conceptual models that are capable of making testable hypothesis within the uncertain domains of biosecurity risk assessment. The project was also able to demonstrate that, by virtue of their graphical format, these methods are amenable to stakeholder input and thereby provide an excellent way to build consensus amongst stakeholders and thereby legitimise the risk-based decision making process. We believe that these techniques therefore provide a sound scientific basis for biosecurity risk assessment.

REFERENCES

AFFA. 2003. Import Risk Analysis Handbook. Department of Agriculture, Fisheries and Forestry, Biosecurity Australia, Canberra.

Ascioti F., C.J. Puccia. 1988. Paradoxical growth in the Messina Strait: Models and Explanations. *In* Advances in Environmental Modelling, Marani E. (*ed*.). Elsevier: Amsterdam; pp. 353–372.

Austin, M.P., J.G. Pausas, I.R. Noble. 1997. Modelling environmental and temporal niches of eucalypts. Pages 129–150 in J.E. Williams, J.C.Z. Woinarski (*eds*). Eucalypt Ecology. *Cambridge University Press*, Cambridge, MA.

Borer, E.T., C.J. Briggs, W.W. Murdoch, S.L. Swarbrick. 2003. Testing intraguild predation theory in a field system: does numerical dominance shift along a gradient of productivity? *Ecology Letters* **6**:929–935.

Borer, E.T., W.W. Murdoch, S.L. Swarbrick. 2004. Parasitoid coexistence: linking spatial field patterns with mechanism. *Ecology* **85**:667–678.

Borsuk M.E., P. Reichert, A. Peter, E. Schager, P. Burkhardt-Holm. 2006. Assessing the decline of brown trout (*Salmo trutta*) in Swiss rivers using a Bayesian probability network. *Ecological Modelling* **192**: 224–244.

Buhs J.B. 2002. The Fire Ant Wars. *Isis* **93**: 377–400.

Burrows, G.E. 2002. Epicormic strand structure in *Angophora*, *Eucalyptus* and *Lophostemon* (Myrtaceae)—implications for fire resistance and recovery. *New Phytologist* **153**:111–131.

Cain, J. 2001. Planning Improvements in Natural Resources Management. Centre for Ecology and Hydrology, Wallingford, Oxfordshire, UK.

Dahlsten, D.L. and Garcia R. 1989. Eradication of Exotic Pests. *Yale University Press*, New Haven, CT.

Dambacher, J.M., H.W. Li, P.A. Rossignol. 2002. Relevance of community structure in assessing indeterminacy of ecological predictions. *Ecology* **83**:1372–1385.

Dambacher, J.M., H.-K. Luh, H.W. Li, P.A. Rossignol. 2003a. Qualitative stability and ambiguity in model ecosystems. *American Naturalist* **161**:876–888.

Dambacher, J.M., H.W. Li, P.A. Rossignol. 2003b. Qualitative predictions in model ecosystems. *Ecological Modelling* **161**:79–93.

Dambacher, J.M, R. Ramos-Jiliberto. 2007. Understanding and predicting effects of modified interactions through a qualitative analysis of community structure. *Quarterly Review of Biology* **82**(3):227–250.

Drees B. M., Barr C. L., Shanklin D. R., Pollet D. K., Flanders K. and Sparks B. (1998) Managing Fire Ants in Agriculture. Texas Agricultural Extension Service Bulletin B-6076.

Texas AM University Press, College Station, TX.

Ferreira, F.A. 1983. *Eucalyptus* rust. *Revista Arvore* **7**:91–109.

Giavelli G., Bodini A. 1990. Plant–ant–fungus communities investigated through qualitative modelling. *Oikos* **57**:357–365.

Gibbs, M. 2007. Application of a Bayesian network model and a complex systems model to investigate risks of a proposed aquaculture development on the carrying capacity of shorebirds at the Miranda Ramsar Wetland. Enviroment Waikato Technical Series 2007/04. Hamilton East, New Zealand.

Gil, A.M. 1997. Eucalypts and fire: interdependent or independent? *Pages* 151–167 *in* J.E. Williams, J.C.Z. Woinarski (*eds*). Eucalypt Ecology. Cambridge University Press, Cambridge, MA.

Glen, M., A.C. Alfenas, E.A.V. Zauza, M.J. Wingfield, C. Mohammed. 2007. *Puccinia psidii*: a threat to the Australian environment and economy – a review. *Australian Plant Pathology* **36**:1–16.

Henrion, M., J.S. Breese and E.J. Horvitz. 1991.Decision Analysis and Expert Systems, *Artificial Intelligence Magazine* **12**(4):64-91.

Hosack G.R., K.R. Hayes, J.M. Dambacher. *In Prep*. Assessing uncertainty in the structure of ecological models through a qualitative analysis of system feedback and Bayesian belief networks.

Kirkpatrick, J.B. 1997. Vascular plant-eucalypt interactions. *Pages* 227–245 *in* J.E. Williams, J.C.Z. Woinarski (*eds*). Eucalypt Ecology. Cambridge University Press, Cambridge, MA.

Kuikka S., M. Hilden, H. Gislason, H. Sparholt, O. Varis. 1999. Modelling environmentally driven uncertainties in Baltic cod management by Bayesian influence diagrams, *Canadian Journal of Fisheries and Aquatic Sciences* **56**:629–641.

Lane P. 1998. Assessing cumulative health effects in ecosystems. In Ecosystem Health, Raport D, Costanza R, Epstein P, Gaudet C, Levins R. (eds). Blackwell Science: MA; 129–153.

Levins R. 1974. The qualitative analysis of partially specified systems. *Annals of New York Academy Sciences* **231**: 123–138.

Levins R. 1975. Evolution in communities near equilibrium. *Pages* 16–50 *in* Ecology and Evolution of Communities. Cody M, Diamond J. (*eds*). Harvard University Press: MA.

Li H., Moyle P. 1981. Ecological analysis of species introductions into aquatic systems. Transactions of American Fisheries Society 110: 772–782.

Li H., Rossignol P., Castillo G. 1999. Risk analysis of species introduction: insights from qualitative modeling. In Nonindigenous Freshwater Organism: Vectors, Biology, and Impacts, Cladi R, Leach J (eds) Lewis: FL; 431–447.

Loiselle, S., G.M. Carpaneto, V. Hull, T. Waller, C. Rossi. 2000 Feedback analysis in reserve

management: studying local myths using qualitative models. *Ecological Modelling* **129**: 25–37.

Marcot, B.G., R.S Holthausen, M.G. Raphael, M.M. Rowland, M.J. Wisdom. 2001. Using Bayesian Belief Networks to Evaluate Fish and Wildlife Population Vialbility Under Land Management Alternatives from and Environmental Impact Statement. *Forest Ecology and Management* **153**:29-42.

Marcot, B.G., P.A. Hohenlohe, S. Morey, R. Holmes, R. Molina, M.C. Turley, M.H. Huff, J.A. Laurence. 2006. Characterizing Species at Risk II: Using Bayesian Belief Networks as Decision Support Tools to Determine Species Conservation Categories Under the Northwest Forest Plan. *Ecology and Society* **11**(2):12. [online] URL: http://www.ecologyandsociety.org/vol11/iss2/art12/.

Marcot, B.G., Stevenson, J.D., Sutherland, G.D., McCann, R.K. 2006. Guidelines for Developing and Updating Bayesian Belief Networks Applied to Ecological Modelling and Conservation. *Canadian Journal of Forestry Research* **36**:3063-3074.

McCaw, W.L., R.H. Smith, J.E. Neal. 1994. Stem damage and crown recovery following high intensity fire in a 16-year-old stand of *Eucalyptus diversicolor* and *Eucalyptus muelleran*a. *Australian Forestry* **57**:76–81.

Murdoch, W., C.J. Briggs, S. Swarbrick. 2005. Host suppression and stability in a parasitioid-host system: experimental demonstration. *Science* **309**:610–613.

Nattrass R., C. Vanderwoude. 2001. A preliminary investigation of the ecological effects of Fire ants (*Solenopsis invicta*) in Brisbane. *Ecological Management and Restoration* **2**:220–223.

OCPPO. In prep. *Puccinia psidii*: forestry, rural, and urban biosecurity plan. Office of the Chief Plant Protection Officer, Department of Agriculture Fisheries and Forestry, Canberra.

Ortiz. M. 2002. Qualitative modelling for the development of a sustainable management strategy for the Peruvian scallop *Argopecten purpuratus* (Lamarck 1819). *Aquatic Conservation: Marine and Freshwater Ecosystems* **12**:273–287

Pearl, J. (2000) Causality: Models, Reasoning, and Inference. Cambridge University Press, UK.

Pollino, C.A., O. Woodberry, A. Nicholson, K. Korb, B.T. Hart. 2007. Parameterisation and evaluation of a Bayesian network for use in an ecological risk assessment. *Environmental Modelling and Software* **22**(8):1140-1152.

Porter, S.D., D.F. Williams, R.S. Patterson, H.G. Fowler. 1997. Intercontinental differences in the abundance of *Solenopsis* fire ants (Hymenoptera: Formicidae): escape from natural enemies? *Environmental Entomolog*y: **26**(2):373-384.

Puccia, C.J., R. Levins. 1985. Qualitative Modeling of Complex Systems: An Introduction to Loop Analysis and Time Averaging. *Harvard University Press*, Cambridge, MA.

Quirk, J., R. Ruppert. 1965. Qualitative economics and the stability of equilibrium. *Review of Economic Studies* **32**:311–326.

Scanlan, J.C., C. Vanderwoude. 2006. Modelling the potential spread of *Solenopsis invicta*

Buren (Hymenoptera: Formicidae) (red imported fire ant) in Australia. *Australian Journal of Entomology* **45**:1–9

Solley, G.O., C. Vanderwoude, G.K. Knight. 2002. Anaphylaxis due to Red Imported Fire Ant sting. *Medical Journal of Australia* **176**:521–523.

Suter, G.W. 1999. Developing Conceptual Models for Complex Ecological Risk Assessments, *Human and Ecological Risk Assessment* **5**:375–396.

Tommerup, I.C., A.C. Alfenas, K.M. Old. 2003. Guava rust in Brazil—a threat to *Eucalyptus* and other Myrtaceae. *New Zealand Journal of Forestry Science* **33**:420–428.

Tschinkel, W. R. 1993. Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. *Ecological Monographs* **64**: 42557.

Uusitalo, L. 2007. Advantages and challenges of Bayesian networks in environmental modelling. *Ecological Modelling* **203**:312–318.

Varis, O Kuika, S. 1997. Bayesian Decision Analysis for Environmental and Resource Management. *Environmental Modelling and Software* **12**(2-3):177–185.

Varis, O, Kuika, S. 1999 Learning Bayesian decision analysis by doing: lessons from environmental and natural resources management. *Ecological Modelling* **119**:177–195.

Vinson, S.B., W.P. McKay. 1990. Effects of the fire ant, *Solenopsis invicta* on electrical circuits and equipment. *Pages* 496–503 *in* R.K. Vander Meer, K. Jaffe, A. Cedeno (*eds*), Applied Myrmecology: A World Perspective, *Westview Press*, Boulder, CO.

Vinson, S.B. 1997. Invasion of the red imported fire ant (Hymenoptera: Formicidae): spread, biology, and impact. *American Entomologist* **43**:23–39.

Williams, J.E., A.M. Gill. 1995. The impact of fire regimes on native forests in eastern NSW. Environmental Heritage Monograph Series. NSW National Parks and Wildlife Service, Sydney.

Wintle, B.A., M.A. McCarthy, K.M. Parris, M.A. Burgman. 2005. Estimating and dealing with detectability in occupancy surveys for forest owls and arboreal marsupials. *Journal of Wildlife Management* **69**(3):905-917.

Withers, J.R., D.H. Ashton. 1977. Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. I. The structure and regeneration. *Australian Journal of Botany* **25**:623–637.

Withers, J.R. 1978a. Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. II. The differential seedling establishment of *Eucalyptus ovata* Labill. and *Casuarina littoralis* Salisb. *Australian Journal of Botany* **26**:465–483.

Withers, J.R. 1978b. Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. III. Comparative water relations of the major tree species. *Australian Journal of Botany* **26**:819–835.

Withers, J.R. 1979a. Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove,

Victoria. IV. The effect of shading on seedling establishment. *Australian Journal of Botany* 27:47–66.

Withers, J.R. 1979b. Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. V. The interactive effects of droughting and shading on seedlings under competition. *Australian Journal of Botany* **27**:285–300.

Whitlatch, R., R. Osman. 1994. A qualitative approach to managing shellfish populations: assessing the relative importance of trophic relationships between species. *Journal of Shellfish Research* **13**(1): 229–242.

APPENDIX A   QUALITATIVE MODELLING METHODS

As in illustrative example, we consider a signed digraph of a three variable system involving the red scale *Aonidiella aurantii*, which is a common non-native insect pest of citrus crops in California:
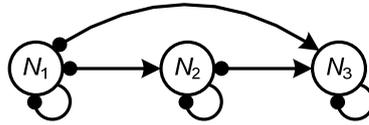
Once the structure of a system is defined then it is possible to analyse the system's feedback which determine the qualitative conditions for system stability and perturbation response. These methods can proceed via analysis of the signed digraph through graphical algorithms or through equivalent algebraic analyses of the system's community matrix. In this work we proceed with analysis of signed digraphs, and present only the basic principles required to understand our analyses; Appendix 1 is a more detailed treatment of the mathematics involved; see also Levins 1975, Puccia and Levins 1985, Dambacher et al. 2002 and 2003a, and Dambacher and Ramos-Jiliberto (2007)—additionally, computer programs for qualitative analyses can be found in the most recent revision of Supplement 1 of Dambacher et al. (2002) in *Ecological Archives* E083-022-S1 at http://www.esapubs.org/archive/.

System stability.—Our first task is to identify whether the model system is sign stable (Quirk and Ruppert 1965), such that its stability is assured no matter what parameter space the system occupies, or if the system's stability is conditional, in which case its stability depends on specific symbolic inequalities. The stability of a system can be judged and understood according to two criteria that depend on the relative sign and balance of the system's feedback cycles (Levins 1974 and 1975, Puccia and Levins 1985, Dambacher et al. 2003a). In general, stability requires that 1) the net feedback in a system is negative, and that 2) feedback at lower levels in the system is stronger than feedback at higher levels in the system. Negative feedback ensures that a system's dynamics are self damped, and stronger feedback at lower levels ensures that a system will not overcorrect and exhibit unrestrained oscillations. For the above example model, stability depends on the relative weakness of feedback cycles involving parasitism by N_3, *A. melinus*. Here the feedback cycle $+a_{3,1}a_{1,2}a_{2,3}$ has the potential to destabilize the system through positive feedback, and the feedback cycle $-a_{2,1}a_{1,3}a_{3,2}$, even though it is negative in sign, has the potential to introduce excessive higher level feedback if it is too strong.

As system size and complexity increases, the symbolic contingencies underlying the conditions for stability in any one model quickly become too complex to reasonably interpret. To address this problem, Dambacher et al. (2003a) developed a set of stability metrics that can be used to judge potential stability in large complex models.

The first of these applies to what are termed class I models. A class I model is characterized by its being prone to failing the first stability criterion through excessive positive feedback. Potential stability in class I systems is judged by the weighted feedback metric wF_n, which is a measure of the net to total number of cycles at cycles at the highest level in the system—i.e., feedback cycles that involve n number of links. Values of wF_n range between -1 and $+1$. A value of -1 indicates all feedback cycles are negative and thus there is no possibility for instability by the first stability criterion. A value of zero indicates an equal number of positive

and negative feedback cycle. Given no information about specific conditions in the system, the probability of stability is that of a coin toss. Based on simulation results (Dambacher et al. 2003a), values of $wF_n < -0.5$ have a relatively high potential for stability.

Class II models are judged by a weighted determinant $w\Delta_{n-1}$, which is a measure of the balance between higher and lower levels of feedback in the system measured through the penultimate (n-1) Hurwitz determinant (Dambacher et al. 2003a). Weighted determinants cannot be compared between systems of different size due to the factorial increase in terms of the determinant with n. Interpretation of this metric proceeds by comparison to the n-1 weighted determinant of a standard "model-c" type system, which is simply a straight chain predator prey model with self-regulation at the basal variable only. We thus develop the metric $w\Delta^C_{n-1}$, which is the ratio of the weighted determinant of the model in question to that of a c-type system of the same size. Values of this ratio great than 1.0 indicate that there is relatively low probability that the model will fail due to excessive higher level feedback, while values approach zero have an increasing likelihood of instability.

The above example system is a class I system with $wF_n = -0.67$, thus it has a high potential for stability. If the above example system was self regulated only at its basal variable N_1, and if there was no positive direct effect between N_1 and N_3, then it would become a class II system. Such a model completely lacks positive feedback, yet it is dominated by higher level feedback through the cycle $a_{3,1}a_{2,3}a_{1,2}$. The value of $w\Delta^C_{n-1}$ in this model equals zero, with stability depending on $a_{3,1}a_{2,3}a_{1,2} < a_{1,1}a_{2,3}a_{3,2}$.

Perturbation response.—We next seek to predict how population levels in the system change as a result of a sustained change to a rate of birth, death or migration of one of the species (Levins 1975, Puccia and Levins 1985, Dambacher et al. 2002). As an example perturbation scenario we consider a positive input to N_2, such as food supplementation that increases its rate of birth, or a shift in some environment factor that decreases its rate of death. The qualitative effect of this input to the other variables is determined by accounting for all of the feedback cycles of length n-1 that emanate from N_2. This is accomplished by tracing all paths from the input variable to a responding variable and multiplying each path by its complementary subsystem, the resulting product is defined as a feedback cycle. The complementary subsystem is defined by the feedback of the variables not on the path from the input to the response variable. If the sign of this subsystem's feedback is positive then it will switch the sign of the path to the response variable, otherwise the sign of the path will be unchanged. The signed digraphs below illustrate the formation of feedback cycles that are used to predict perturbation response. All links that enter the input variable and all links leaving the response variable have been removed; products of the remaining links then become the feedback cycles which determine the sign of the response. For response of N_1 feedback cycles will be composed of the following links:
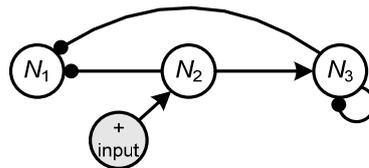
Here two feedback cycles determine the sign of the response of N_1 due to an input to N_2. One feedback cycle, $-a_{1,2}a_{3,3}$, is formed by a path which goes directly from N_2 to N_1, and it has a

complementary subsystem in the negative self-effect of N_3. The other cycle, $-a_{1,3}a_{3,2}$, is composed of path with negative sign of length two. This path lacks a complementary subsystem, in which case the sign of the path remains negative. Since both feedback cycles are negative, the equilibrium abundance of N_1 is predicted to decrease as a result of supplementation of N_2.

Next we consider the response of N_3 when there has been a negative input to N_2, say through an increased rate of death through culling, and note that for negative inputs the sign of the feedback cycles are switched. The sign of the response of N_3 is determined by the following links

,
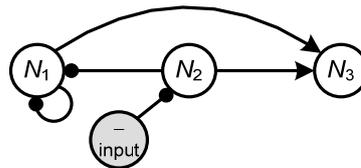
which form feedback cycles $+a_{1,2}a_{3,1}$ and $-a_{3,2}a_{1,1}$. Here the response is ambiguous, as it is determined by feedback cycles of opposing sign.

The ambiguity in the response of N_3 can be resolved through consideration of symbolic inequalities. For instance, if it is believed that $a_{3,2}a_{1,1}{>}a_{1,2}a_{3,1}$, then the predicted response of N_3 will be negative. Dealing with ambiguity in this manner requires a relative knowledge of interaction strengths, and an ability to make sense of contingencies presented by symbolic arguments.

In small systems ($n < 7$) the above described graphical procedures can be applied with relative ease, but as system size and complexity increases it becomes difficult to keep track of all possible paths and products of complementary subsystems. In these instances we can proceed by matrix methods described by Dambacher et al. (2002), and consider analysis of the adjoint (adj) of the negative community matrix. For our above example system, the adjoint matrix is

$$\text{adj}(-A) = \begin{bmatrix} a_{2,2}\,a_{3,3} + a_{2,3}\,a_{3,2} & -a_{1,2}\,a_{3,3} - a_{1,3}\,a_{3,2} & a_{1,2}\,a_{2,3} - a_{1,3}\,a_{2,2} \\ a_{2,1}\,a_{3,3} - a_{2,3}\,a_{3,1} & a_{1,1}\,a_{3,3} + a_{3,1}\,a_{1,3} & -a_{1,1}\,a_{2,3} - a_{1,3}\,a_{2,1} \\ a_{2,1}\,a_{3,2} + a_{2,2}\,a_{3,1} & a_{1,1}\,a_{3,2} - a_{1,2}\,a_{3,1} & a_{1,1}\,a_{2,2} + a_{2,1}\,a_{1,2} \end{bmatrix}.$$

The results of a press perturbation to the second variable is read down the second column of this matrix, and for a negative input the sign of the matrix elements are reversed. In larger systems, complex inequalities can arise that are too difficult to interpret or comprehend symbolically. In these instances we can derive the same calculation using the signed unity of the community matrix elements, such that entries are either +1, –1, or 0. This kind of community matrix is denoted by $^\circ\mathbf{A}$, and its adjoint for the above system is

$$\text{adj}(-^\circ\mathbf{A}) = \begin{bmatrix} 2 & -2 & 0 \\ 0 & 2 & -2 \\ 2 & 0 & 2 \end{bmatrix}.$$

Ambiguous predictions from this matrix can be interpreted through a technique of weighting the net number of feedback cycles to the absolute number in a response—i.e., the *weighted*

prediction for a response prediction is equal to the net number of feedback cycles divided by the total number of cycles (Dambacher et al. 2002). For instance, the predicted response of N_3 for an input to N_2 is completely ambiguous, as there is the same number of positive and negative feedback cycles. But if there were, say, a total of four feedback cycles in a perturbation response, three of which were positive and one negative, then the net number of cycles would be two and the weighted prediction of the response would be 2/4 = 0.5. The sign determinacy of responses with weighted predictions ≥0.5 has been shown to generally be >90% through simulations using random parameter space (Dambacher et al. 2003b); below this threshold the sign determinacy of responses declines to zero for weighted predictions equal to zero. In Hosack et al. (in prep.) we have attributed a probability for sign determinacy to adjoint matrix predictions, and in results discussed below we present adjoint matrices along side a matrix detailing the potential sign determinacy of each adjoint matrix element .

APPENDIX B   RIFA MANAGEMENT VARIABLES

The following variables were identified by a literature search of RIFA biology and the factors that might govern the successful eradication of RIFA nests:

- Management Strategy

"Whichever management strategy is chosen, it is extremely important to choose appropriate methods to do the job and to undertake the work in the right season of the year. Most pest management methods work better at one time of the year than another and there may even be times when they are totally ineffective. Some methods will work well on one species at one time of year but for another species the same method will have to be used at a different time of year. A related topic is, which stage of the invader is most vulnerable to management methods."
('Global Invasive Species program http://www.gisp.org/)

- Season - Fire ant populations are known to fluctuate from season to season (Tschinkel, 1993)

- RIFA Density – Porter et al. (1997) use "total volume of mounds per hectare" as the primary measure of fire ant density.

- RIFA Biology

"The mounds are often located in rotting logs and around stumps and trees. Ant colonies can also be found in or under buildings. Two types of mounds exist: single-queen colonies where there are typically 30 to 100 colonies per acre, and multiple-queen colonies where the density of mounds per acre may average between 200 and 700, with each mature colony having 200,000 ants" (www.attra.ncat.org)

"The presence of polygyne fire ant colonies generally increases fire ant densities by 2 to 3 fold in the United States. Fire ants spread in two ways, according to the type of colony. From the single-queen colonies, winged virgin queens emerge, fly high above the colony, and mate with winged males between spring and early fall. The queens land to establish new colonies alone. Such airborne spread should lead to a patchy distribution of new fire ant colonies interspersed with colonies of native ant species. Multiple-queen colonies spread when a new queen leaves the parent mound with a group of workers to form a new colony nearby" (Porter et al., 1997)

- Habitat Complexity

"The red imported fire ant prospers in open sunny areas such as cropland, pastures, and urban lawns. It is an insect of disturbed, low-diversity habitats. In its native South America, the ant evolved in frequently disturbed floodplain areas. Undistarbed areas, such as swamplands and dense forests, have very low densities of fire ant nests. The ants have an aversion to deep shade". (www.attra.ncat.org)

APPENDIX C   PEST MANAGEMENT STRATEGIES

The GISP Toolkit of Best Prevention and Management Practices (www.gisp.org) suggests that there are four main strategies for dealing with established invasive alien species:

- Eradication

- Containment

- Control

- Mitigation.

When prevention measures have failed, an eradication programme is considered to be the most effective action, because of the opportunity for complete rehabilitation of the habitat. Since eradication programmes are usually very costly and need full commitment until completion, the feasibility of eradication needs to be carefully and realistically assessed beforehand. Eradication has been achieved using mechanical, chemical and biological control, as well as habitat management. Although examples of successful eradication feature in most taxonomic groups, most success has been achieved against land vertebrates on small islands.

Containment is a specific form of control. The aim is to restrict an invasive species to a limited geographical range. The population can be suppressed using a variety of methods along the border of the defined area, individuals spreading outside this area are eradicated, and introductions outside the area prevented.

Control of invasive alien species should be planned to reduce the density and abundance of the target to below an agreed threshold, lowering the impact to an acceptable extent. The suppression of a population will reduce its competitiveness and, under optimal conditions, native species will regain ground and replace the invasive species.

Mitigation as used in this context differs from containment and control in that the activity undertaken does not directly affect the invasive species in question but rather focuses on affected native species. If eradication, containment, and control are not options or have failed in managing an invasive alien species, the last resort is to "live with" this species in the best achievable way and mitigate impacts on biodiversity and endangered species. Mitigation is most commonly used in the conservation of endangered species and can be approached at various levels. At its simplest and perhaps most extreme form it could mean the translocation of a viable population of the endangered species to an ecosystem where the invasive species of concern does not occur or, in the case of a rehabilitated system, no longer occurs.